INTERACTIONS AMONG <u>ATTALEA</u> PALMS, BRUCHID BEETLES, AND
NEOTROPICAL TERRESTRIAL FRUIT-EATING MAMMALS: IMPLICATIONS
FOR THE EVOLUTION OF FRUGIVORY

By

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To Joe,

without whose imagination

creativity

determination

bullying

cajoling

loving

laughing

and, of course, canoeing

none of this would have been possible

or even desirable.

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The staff at Maracá Island Ecological Reserve ensured the smooth running of the station and comfortable living conditions in a remote place. Station Manager Guttemberg Moreno de Oliveira did his best to understand the nature of our research and relied on his love of Maracá to navigate the political storms that threaten research in places like Roraima. A consummate humanist, when push came to shove he always did the right thing for his friends.

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The fruits and seeds of arborescent palms are important
food items in the diet of Neotropical terrestrial mammals.
A literature review shows that seventy-seven species of
mammals have been documented feeding on fifty-nine species of
palms. Most of the records are of pulp rather than seed
consumption. Among mammals, terrestrial consumers are the
most important predators and dispersers of palm seeds.
Bruchid beetles (Coleoptera: Bruchidae: Pachymerini) are
specialized predators on palm seeds and are associated almost
exclusively with the coconut-like palms (tribe Cocoeae).

Manipulation of Attalea palm fruits indicated that pulp
removal by rodents, primates, and ungulates improves fruit
quality for ovipositing bruchid beetles. Fruits that fall to
the ground unhandled by any vertebrate have the best chance

of surviving beetle infestation: they are rapidly removed by tapirs (_Tapirus terrestris_) and are later defecated at sites where infestation by bruchids is lower than near parent trees.

Monitoring of palm endocarp use by white-lipped peccaries (_Tayassu pecari_), agoutis (_Dasyprocta agouti_), and squirrels (_Sciurus igniventris_) indicates that all three species feed on bruchid beetle larvae. Squirrels are palm specialists that feed on both larvae and endosperm year round; agoutis feed on both larvae and seeds only at times and at sites where alternate foods are not available; and white-lipped peccaries feed preferentially on bruchid larvae rather than seeds. The three species should therefore respond independently and distinctly rather than as a community to changes in _Attalea_ fruit availability.

Home range size of five radio-collared agoutis ranged from 2.9 to 8.5 ha. All animals showed a shift in core area use as different individuals of the same tree species and individuals of different tree species came into fruit. Agoutis responded to their habitat at the scale of individual trees, and appeared to base foraging decisions on knowledge of food available on their entire home range. Preferred diet items were primarily in the Sapotaceae (_Pouteria surumuensis_ and _Pradosia surinamensis_) and secondarily in the Palmae (_Astrocaryum aculeatum_ pulp and seeds and _Attalea maripa_ pulp).

Arborescent palms, a widespread and abundant group of plants with a fairly coherent fruiting biology, are an important source of food for Neotropical forest mammals. Palm fruits are staples in the diet of some species at some study sites (ungulates, Bodmer 1989a,b; squirrels, Glanz et al. 1996) and have been proposed as "key" or "keystone" food species for frugivorous mammals (Terborgh 1986a,b, Spironelo 1991, Peres 1994a) at other sites. Due to their abundnace and importance in frugivore diets, palms can serve as easily studied models of the evolution and ecology of frugivory systems. Their importance in the diet of terrestrial mammals in particular may help us understand the role of these poorly studied species in seed dispersal, seed predation and forest regeneration. However, the unique life history characteristics of palms must be understood before the results of palm ecology studies can be extrapolated to tropical frugivory systems in general.

Palm-mammal interactions have been studied in detail at only a few Neotropical sites. As an introduction to a detailed study of the interactions between one palm species and its mammalian consumers, in Chapter 2 I review the current state of knowledge and assumptions about the

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importance of palms to fruit- and seed-eating Neotropical forest mammals. The remainder of the dissertation focuses on the ecology of one palm, <u>Attalea maripa</u>, and examines 1) the implications of the spatial distribution of trees for fruit availability to animals operating at different spatial scales and 2) the role of insects in fruit-vertebrate interactions.

Chapters 3 and 4 focus on two aspects of the interaction among bruchid beetles, <u>Attalea maripa</u> palms, and vertebrate fruit and seed consumers. Chapter 5 addresses the effect of the spatial distribution of the palms, within several forested habitats, on the pattern of food availability for one species of terrestrial fruit and seed eating mammal: the agouti, <u>Dasyprocta agouti</u>. Throughout, I address three components of frugivory theory: the role of keystone food resources in structuring frugivore communities; the effect of patchiness in food distribution on animal movements and demography; and the contribution of plant-animal interactions to the patchy distribution of plant species.

CHAPTER 2
PALM FRUITS AND NEOTROPICAL RAIN FOREST MAMMALS: DIRECT AND
INDIRECT RELATIONSHIPS

<u>Neotropical Palm Use by Mammals</u>

Neotropical arborescent palms produce fruits that in
their size and color fit the classical mammal dispersed fruit
syndrome, as defined by van der Pijl (1982). The fruits can
be large (e.g., 5 cm diameter for <u>Mauritia</u> <u>flexuosa</u>, 7 cm
length for <u>Attalea</u> <u>maripa</u>; van Roosmalen 1985), with a
nutritious oily or sweet mesocarp (pulp). The seed is
usually protected by a thick endocarp (nut wall) of up to 0.5
cm in thickness. The exocarp (husk) and mesocarp are usually
yellowish, orange, reddish-brown, or brown in color (Uhl and
Dransfield 1987, van Roosmalen 1985). Some medium sized
(< 20 m tall) and understory palms also produce similar
fruits. Other small palms produce fruits that seem better
adapted for bird dispersal due to the small size of their
seeds and the red color of the fruits (e.g., <u>Bactris</u> spp.),
although their fruits are also ingested by primates and their
seeds dispersed after passage intact through the gut (e.g.,
<u>Desmoncus</u>, van Roosmalen 1985).

Currently, the Neotropical palm fruit- and seed-eating
fauna disperses seeds either by ingesting them along with the

fruit and passing them intact through the gut (e.g., tapirs), by spitting out the seeds after eating the pulp (e.g., tapirs and some primates), or by scatter-hoarding seeds (e.g., Dasyprocta and other rodents; Smythe 1986, van Roosmalen 1985). Terrestrial rather than arboreal frugivores and granivores tend to be the most important seed predators and dispersers for palms, using the pulp or seeds or both after they have fallen to the ground. Few mammals except for some primates and occasionally squirrels seem to harvest the fruits or seeds from the tree itself. Macaws appear to be the only important avian consumers of large palm fruits and seeds (Munn 1988). The only true palm specialist among them, the Hyacinth macaw (Anodorhynchus hyacinthinus), also feeds on palm seeds from the ground in the open Pantanal habitat (Munn et al. 1990). The ecological interactions between large palm fruits and terrestrial consumers suggest that palm fruit use by terrestrial frugivore/granivores represents more than just the use of residual fruit production. Examination of the foraging ecology of terrestrial fruit eaters may bring new insight to the study of frugivory, since paradigms in this field are based almost completely on work done with birds and primates.

Seasonal and supra-annual variation in levels of fruit availability can determine the carrying capacity for frugivorous animals, as well as lead to the evolution of behavioral, physiological, and morphological adaptations to deal with food shortages (Eisenberg 1980, Terborgh 1986a,b,

Leighton and Leighton 1983, Malcolm 1990, Caldecott 1992, van Schaik et al. 1993, Leigh et al. 1996). Any mammals that have become palm specialists or that rely heavily on palm fruits will see their population dynamics affected by the spatiotemporal patterns of palm fruit availability in their habitat. Although there are few studies on the fruiting phenology of arborescent palms, three studies of palm fruiting at the community level (de Steven et al. 1987, Sist 1989, Peres 1994b) and one population level study (Piñero and Sarukhan 1982, Piñero et al. 1984) demonstrate that there is great seasonal and supra-annual variability in the likelihood of reproduction of individual palms and palm patches alike. The predictability of these production patterns is unknown, but palms do not appear to be more reliable a fruit source than other tropical fruiting trees. Recent data from Barro Colorado Island, Panama (BCI; J. Wright pers. comm.) indicate that large and small fruited palms participate along with dicots in forest-wide fruit peaks and failures following El Niño Southern Oscilation events.

The same factors that make palm fruits attractive to other mammals--nutritious pulp and seeds--also make them highly attractive to humans. Native human populations traditionally have used palms for their fiber, stem tissue, and sap as well as for their fruits (Balick 1988). Thus their current ecology has been affected by at least several thousand years of interactions with humans, which can affect

distribution and fruit traits (e.g., domestication of _Bactris_
gassipaes) (Balée 1988, Anderson et al. 1991).

For this review I surveyed the Neotropical ecological
literature to extract the following information: Which
mammals are known to use palms? Numerically, how important
are palms in the diets of these animals? Since seeds are a
long lasting resource and pulp a more ephemeral one, which
part of the palm fruit is most heavily used? What is the
nature of the interaction among palms, bruchid beetles
specialized on palms, and vertebrate palm consumers? What
are the ecological and evolutionary implications of these
interactions?

Methods

The literature summarized here is a biased sampling of
the information available on palm-mammal interactions,
because it does not include many articles published in Latin
American journals. It does however include unpublished
theses from Latin American universities and unpublished data
from several Latin American researchers. From each source I
obtained the following information: the palm species used by
mammals, the mammal species using palms, the part of the palm
fruit used, the location of the study, and notes on the
behavior of the mammals, in particular whether they seemed to
be using the palm as a keystone resource in the season of
fruit scarcity (sensu Terborgh 1986a,b). For studies that

lasted about a year or more and gave information on the
dietary composition of the study species I summarized the
importance of palm fruits as the proportion contributed to
the diet. Most of the studies reported here took place in
humid forest, some in deciduous or dry forest, and a few in
open habitats. I do not include information on use of any
palm parts other than pulp and seeds, although meristem and
flowers are reported as important resources for many mammals,
as are the arthropod populations that shelter in palms and
which are heavily used by insectivorous or omnivorous
arboreal and scansorial mammals, particularly primates. The
available literature on palm bruchids is limited to
ecological studies at a few Neotropical sites (BCI, Maracá
Island Ecological Reserve in northern Brazil, and a few brief
studies in Costa Rica, Peru, and Bolivia.)

Results and Discussion, Palm-Mammal Interactions

General Trends

At least 77 species of mammals in 44 genera were
reported to feed on palm pulp or seeds from 59 species of
palms (excluding potential synomyms and species identified to
genus only; Table 2-1). Five of these mammals species are
from non-forested habitats, leaving a total of 72 mammals
reported using palm fruits in Neotropical forests, either
humid or dry. It is likely that many of the mammals listed

in Table 2-1 will feed on palms whenever they co-occur with them, even though they have not been reported to do so in the literature (e.g., the larger marsupials are only described as eating palms at two sites, but they probably do so throughout their range).

The five most frequently cited genera in Table 2-1 are reported from a limited number of study sites: _Cebus_ (4 sp., 10 sites), _Ateles_ (3 sp., 7 sites), _Tayassu_ (2 sp., 6 sites), _Sciurus_ (7 sp., 7 sites), _Dasyprocta_ (2-3 sp., 4 sites). The best represented orders are primates (19 species) and rodents (29 species), followed by ungulates (Perissodactyla, 2 species, Artiodactyla, 5 species; note that all Neotropical forest ungulate species are represented), marsupials and carnivores (6 species each, but only 2 forest carnivores and 4 forest marsupials). The Chiroptera are last with 2 species and Edentates are represented only by two species mentioned in two studies (one Edentate species in Peru was not identified (Allen 1997).

Conspicuously absent from Table 2-1 are the large fruit bats, _Artibeus_ sp., which are reported only from Trinidad, and the smaller marsupials. In the case of bats, it is likely that their small body size and relatively weak jaws preclude them from using most palm species, as they would be enable to carry away large fruits or to tear away the resistant husks (J. Eisenberg pers. comm.). In the case of marsupials, they are probably absent from consumer lists because their nocturnal habits make them less susceptible to

detection by researchers. Although Bodmer's (1989a,b, 1990, 1991) studies show that all ungulates rely heavily on palms, because ungulates are seldom studied, their interactions with palms in the rest of their range are not reported. In particular, they are not reported from French Guiana, despite the abundance of studies on smaller mammals there.

Members of the Procyonidae probably feed on palms throughout their range. Rainforest canids, if studied, might be found to feed on fallen palm fruits. Canids in two non-forest sites (Brazilian cerrado and Sonoran desert) used palm fruits. Although the most cited order, rodents are under-represented relative to their richness, abundance, and frugivorous/granivorous diet. Only half of the neotropical squirrels are reported, one of three <u>Heteromys</u>, and a few of the Echimydae. The agouti (<u>Dasyprocta</u> sp.), despite its frequency in Central and South America, is reported only from French Guiana, BCI, Maracá, northeast Peru and Belize. In a captive study, Adler (1995) found that <u>Proechimys semispinosus</u> in Central America ate the pulp and seeds of all palm fruits offered, including seeds with very thick endocarps such as <u>Attalea</u>. However, Emmons (pers. comm.) believes that due to their weak jaw structure <u>Proechymis</u> rats are not likely to be significant predators on <u>Attalea</u> palms.

Primates, on the other hand, are well represented, probably due to the large number of detailed studies that have been carried out on their behavior and social structure. At the same time, primates alone among the species listed

have the hand and mouth dexterity necessary to open palm nuts and exploit both the mature seeds and the liquid endosperm. This is illustrated by Izawa's (1979) report of _Cebus apella_ using bamboo sticks to beat and poke open palm fruits, and Struhsaker and Leland's (1977) description of palm nut smashing by the same species.

Evidence for Mammalian Dependence on Palms--Staple Food vs. Keystone Items

Terborgh (1986a) defines keystone resources in Neotropical forests as species that are common in the diets of several members of a frugivore community during periods when little fruit is available, and proposes that such resources help structure Neotropical animal communities. This is a unique usage of the term, distinct from other definitions in the literature (Power et al. 1996, Gilbert 1980); throughout this paper I refer to "keystone species" sensu Terborgh. Based on the use of palm nuts by capuchin monkeys in Cocha Cashu, Peru during the season of food scarcity, Terborgh proposes palms as keystone food resources. He qualifies this proposal, however, by stating that keystone status would hold only "if other consumer species [besides capuchins] are relying on the same resources;" in that case, "the plants that produce these resources can be recognized as playing a critical role in the ecosystem (p. 337)." Here I review the frequency of palm nut versus pulp use during times of fruit scarcity by _Cebus_ and other fruit-eaters.

Pulp was the most frequently cited fruit part eaten by mammals (96 citations, based on a simple count of the number of times each part is listed in Table 2-1). Mature or old seeds followed with 64 citations, then immature seeds and entire fruit with 16 and 20 citations respectively. Fifty two references to palm eating by mammals did not mention the part eaten. Contrary to the emphasis given in the literature to palm seed-rodent interactions and to long-lasting palm nuts as a keystone resource (Terborgh 1986a,b), pulp may be a more important resource than seeds for the frugivore community. However, it is difficult to estimate the true importance of each fruit part, since the amounts of each part eaten are seldom given in the literature.

Few studies of Neotropical rainforest mammals last long enough to cover seasonal changes in food use, let alone supra-annual variation. Even if the data are gathered, they are not always presented in a form from which it is easy to calculate the percent importance of a food item in the diet (e.g., Terborgh 1983). Table 2-2 summarizes the information from a few studies that examined dietary composition to some degree. For five species of ungulates (_Mazama americana_, _M. gouazoubira_, _Tayassu pecari_, _T. tajacu_, _Tapirus terrestris_), Bodmer (1989a) derived the percent composition of the diet from stomach contents gathered over a 15 month study period by local hunters in northeast Peru. All species had at least one palm in the list of the top three diet items, and four of them (_Tayassu tajacu_ was the only exception) had palms as the

top two diet items. It seems that in this area all these species are dependent on palms, but the fact that peccaries at least do well in areas where no palms occur (e.g., Olmos 1993) suggests that they have a fairly flexible diet and that in other areas they may have other major resources. Throughout Amazonia, however, reports from other researchers suggest that palms are important at least for peccaries (Anderson 1983, Fragoso 1993).

In her study of _Ateles belzebuth belzebuth_ on Maracá Island, Roraima, northern Brazil, Nuñes (1992, 1995) found that palms were not an important diet item for this species. One exception was _Attalea maripa_, which during one of the months of fruit scarcity constituted 10.1% of the diet, but it represented only 1.23% of the yearly diet. Even though the fruit was consumed at a time of fruit low, it was the pulp rather than the mature or old endosperm that was consumed. Roosmalen (1980) found an even lower percent importance of palm fruits in the diet of another spider monkey, _Ateles paniscus_, during a two year study in Suriname. On the other·hand, Castellanos and Chanin (1996) found that _A. belzebuth_ in southern Venezuela relied heavily on palms and used them throughout the year in proportion to their abundance.

In general palm use by _Ateles_ is low when compared to palm use by _Cebus_. Buckley's (1983) study of _Cebus capucinus_, where one palm species constituted 58.2% of the diet in October and was the highest ranking diet item for the

entire year. It was eaten during seven months of the year, not just during the season of fruit scarcity. This last figure is comparable to the 64% of diet reported for three months for _Cebus apella_ in Manu, and 56% for _Cebus albifrons_ in the same period (Terborgh 1983). There may thus be a real difference in the degree of palm use by spider vs. capuchin monkeys, but a comparison needs to be made controlling for the abundance of palms in the habitat.

Izawa (1979) comments that palm fruits were usually available for a longer period of time (more asynchrony) than other fruit species, and that in addition primates fed on them before, during, and after they ripened, which increased their period of availability. Primates' ability to use the liquid immature endosperm seems to be one of the traits that makes palms an important resource for them. Observations such as these highlight the importance of clearly documenting the availability of--and distinguishing between--different maturity stages of fruits in phenological studies.

Several studies report that _Cebus_ in other parts of their range turn to palm nuts during the season of scarcity. U. Bobadilla (pers. comm.) documented _Chiropotes_ sp. and _Cebus_ sp. feeding on the pulp of _Attalea speciosa_ (as _Orbignya phalerata_) in the rain forests of western Pará, Brazil, during the period of forest wide fruit low. This case is unusual because the palm fruited during the dry rather than the wet season; similar phenological behavior is reported for _Attalea phalerata_ in the Beni of Bolivia (D.

Quiroga pers. comm.), whereas _Attalea_ palms at study sites north of the Equator tend to fruit in the wet season, generally the peak of forest wide fruit availability. That is the time when _Ateles belzebuth_ fed heavily on _Attalea maripa_ pulp in southern Venezuela (Castellanos and Chanin 1996). Bobadilla suggests that _Attalea speciosa_ may be an asynchronous fruiter at his high rainfall site, but this may be an artifact of low palm densities. (Even when a plant population has a well-marked peak in fruit production, there often are some individuals that fruit outside of the peak. When a plant population occurs at low density, non-peak fruiters may be as well represented in the population or in the samples as peak time fruiters.)

Jessenia (_Oenocarpus_) _bataua_ in the southwestern Amazon (Peres 1994a) produces fruits primarily in the dry season, when other fruits are not available at this site, but also produces some fruits year round. Among the primates, _Cebus apella_ relies heavily on the immature seeds during this time and Peres (1994b) suggests that the palm acts as a key food item. However, he also indicates that _Cebus_ as well as _Pithecia_ and _Lagothrix_ use the immature seeds throughout the year. In Spironelo's (1991) study, palms were also used most frequently in the dry season. _Jessenia_ pulp was used in the dry season, which was also the season of fruit scarcity at that site, while immature seeds were used during the wet season. In Roraima, in the northern Brazilian Amazon, _Astrocaryum aculeatum_ also fruits in the mid-dry season, when

fleshy fruit production is low (Silvius, pers. obs.), but the species is an unpredictable fruiter (Fragoso unpublished data).

In all other cases where palms are used during the period of scarcity, it is the palm seeds that are involved, because they remain available on the ground past the time of low food availability (Terborgh 1986a for <u>Cebus</u>, Smythe et al. 1996 for agoutis, Chapter 4 for agoutis and white-lipped peccaries).

It is clear from Izawa's (1979) and Defler's (1979) studies in Colombia that many primate species seek out the immature and still liquid endosperm during the time that it is abundant and also feed on the pulp of the palms. Struhsaker and Leland (1977) report on another specialized behavior of <u>Cebus</u>, in this case beating the nuts (endocarps) of <u>Astrocaryum</u> <u>chambira</u> against tree trunks, branches, or other nuts, apparently in an attempt to obtain the endocarp contents. I have observed this same behavior by <u>Cebus</u> <u>nigrivitatus</u> on <u>Astrocaryum</u> <u>aculeatum</u> in northern Brazil, but in this case the primates were smashing large preripe intact fruits rather than nuts, and the purpose of the knocking appeared to be to make the hard endosperm easier to remove, because fresh endocarps would be nearly impossible to open by banging (infestation by bruchid beetles, which makes the seeds easier to crack, occurs only on the ground). Norconk et al. (1998) show that among Neotropical primate seed predators, only <u>Cebus</u> has been reported to feed on palm

endocarp contents. It thus appears that <u>Cebus</u> spp. across their range rely heavily on palms throughout the year, and so to some extent may be considered dependent on palms.

This review suggests that a) the use of palms either as staples or as "keystones" *sensu* Terborgh may be unique to the genus <u>Cebus</u> and b) that it is difficult to determine whether the fruits and seeds are being used as staples or "keystones." This does not diminish their importance to mammalian fruit eaters, but it does challenge the idea that "keystone resources" *sensu* Terborgh structure tropical forest communities. The review also suggests that the importance of palms as low season resources is heavily context- and habitat-dependent, and will change with the time of fruiting of the palms and the relative availability of other preferred fruit.

Squirrels appear to be the only true palm specialists in the Neotropics, using palms in large numbers throughout their range. Although they occasionally use the pulp (Table 2-1), most frequently they feed on seeds collected from the ground. On BCI, <u>Astrocaryum standleyanum</u> makes up 21% of the diet of <u>Sciurus granatensis</u> (Glanz et al. 1996; Table 2-2). At Los Tuxtlas, Mexico, two species of <u>Sciurus</u> destroy 20-60% of the fruits of the understory palm <u>Astrocaryum mexicanum</u> in low palm density areas and 75-80% in high palm density areas (Piñero and Sarukhán 1982). In Campinas state, Brazil, <u>Syagrus romanzoffiana</u> alone made up 49% of the diet of <u>Sciurus ingrami</u> (study period unspecified; Galetti et al.

1992). Emmons (1984), based on an accumulation of observations, estimates that about three palm species (_Attalea_ and _Astrocaryum_ groups) make up about 95% of the diet of the large squirrels _S_. _spadiceus_ and _S_. _igniventris_. Because squirrels do not occur at high densities in Amazonia and therefore are not frequently seen (Eisenberg pers. comm.), palm seed use by squirrels is not well documented in the literature. Furthermore, there are no detailed studies of squirrel ecology in the Neotropics (Emmons, pers. comm.).

The potential effect of palm fruit availability on reproductive rates and presumably population sizes of squirrels is suggested by a comparison between BCI and a nearby (30 km away) mainland site (Glanz et al. 1996). On BCI, there are three peaks of squirrel reproduction each year, occurring throughout the time of staggered fruit production by _Dipteryx_, _Astrocaryum_ and _Scheelea_. Mortality for juveniles is highest for the last cohort. On the mainland site, where _Dipteryx_ is absent and _Astrocaryum_ scarce, a single reproductive bout coincides with the period of _Scheelea_ fruit availability. There is no evidence of a similar matching at the supra-annual level.

Results and Discussion: Fruit-Vertebrate-Bruchid Interactions

The previous sections reviewed interactions between vertebrates and palm fruits. For a subset of Neotropical palms, however, these plant-vertebrate interactions intersect

with the use of palm seeds by the palm-specific bruchid beetles (Family Bruchidae, Order Coleoptera). Adult female beetles lay their eggs on the endocarp or mesocarp of fallen fruit, usually at night and usually but not always once the fruits are on the forest floor. After approximately 7 days, the first instar larvae hatch and tunnel through the endocarp to reach the endosperm. The larvae then feed on the endosperm and grow inside the protection of the palm endocarp for approximately two months, finally pupating and emerging as adults through an exit hole carved by the last larval instar. Although several palm families are parasitized in this way, the most intensive parasitism seems to occur among cocosoid palms in the subfamily Arecoideae, which includes the genera _Attalea_ and _Astrocaryum_.

Bruchid-palm interactions are relevant to the above review of palm use by mammals because there is mounting evidence that in many cases mammals feed on bruchid larvae rather than on endosperm when they crack open palm endocarps. The dynamics of larva availability are likely to be different from those of endosperm availability. Only a few authors have recorded vertebrate frugivores or omnivores feeding on bruchid beetle larvae (Robinson 1986, Fragoso 1994), although several have suspected it occurs (Janzen 1971, Strushaker and Leland 1977, Wright 1990). A captive white-lipped peccary offered larvae-infested _Attalea maripa_ endocarps readily cracked all those that were not too thick and ingested the larvae (Fragoso 1994). Terborgh (1983) notes that

individuals of _Cebus_ _albifrons_ in Manu descend to the ground,
pick among fallen _Astrocaryum_ seeds for bruchid infested
ones, crack them open, and pick out the remaining endosperm.
Robinson (1986), on the other hand, noted that _Cebus_
nigrivitattus in the Venezuelan Llanos picked up larvae
infested _Copernicia_ _tectorum_ seeds from the ground and ate
the larvae. Strushaker and Leland (1977) suspected that the
Astrocaryum nuts cracked by _Cebus_ _apella_ in Colombia
contained larvae, because most nuts collected on the ground
were infested. On Maracá, agoutis, squirrels, and white-
lipped peccaries fed on bruchid larvae from _Attalea_ _maripa_
seeds in the wild (Chapter 4). Terborgh (1983) believes that
the _Cebus_ chose infested seeds over uninfested ones because
they were easier to open than solid seeds; this is probably
also a factor on Maracá, especially for white-lipped
peccaries.

Humans in the Neotropics also use bruchid larvae from
palm seeds both as food and as fish bait. They seek these
larvae out from seeds that are usually too hard to eat,
although they prefer the larger larvae obtained from wood-
boring beetles that lay their eggs in rotten palm trunks (for
the Yanomami of Brazil and ribereños in Peru, Silvius, pers.
obs.). Balée (1988) reports that the Arawaté of the eastern
Brazilian Amazon kept bruchid infested palm seeds in their
homes to "raise" the larvae. They then either eat the larvae
or extract oil which they use to soften bow strings.

Research on the biology of palm bruchids falls into three areas: 1) taxonomy, with a recent revision by Nilsson and Johnson (1993); 2) biogeography, with examination of host ranges and overlaps by Delobel et al. (1995) and Johnson et al. (1995); and 3) ecology of plant animal interactions. In the latter area, research has focused on two palm groups: _Astrocaryum_ palms with _Caryoborus_ beetles, and _Attalea_ palms with _Speciomerus_ and _Pachymerus_ beetles. The two palm genera differ significantly in the thickness and texture of their pulp, and the strength and size of their endocarps. Janzen (1971) initiated the research sequence with _Attalea_ palms, focusing on the effect of bruchids on palm demography, but also indicated that there would probably be interactions between beetles and both pulp eaters and seed eaters. Later work followed up on the bruchid-palm tree aspect of the interaction (Wilson and Janzen 1972, Bradford and Smith 1977, Wright 1983, 1990). Three-way interactions were always commented on as peripheral phenomena, but never explicitly studied (with the exception of one short term experiment by Delgado et al. (1997) with the _Astrocaryum_ system.

Palms from the genera _Attalea_, _Scheelea_, _Maximiliana,_ and _Orbignya_ have recently all been grouped in the genus _Attalea_ by Henderson (1995) and I use the revised taxonomy. The taxonomy of bruchid beetles has also recently been revised (Nilsson and Johnson 1993). The name changes of species frequently encountered in the literature are summarized in Table 2-3.

Most long-term ecological work on the palm-bruchid system has been carried out on <u>Attalea</u> <u>butyraceaa</u> (Janzen 1971, Wilson and Janzen 1972, Bradford and Smith 1977, Wright 1983, 1990) and <u>Attalea</u> <u>maripa</u> (Fragoso 1994, 1997), with two additional short term studies on <u>Astrocaryum</u> <u>chambira</u> (Delgado et al. 1997) and <u>Attalea</u> <u>phalerata</u> (Quiroga 1997). <u>Attalea</u> <u>butyracea</u> and <u>A</u>. <u>maripa</u> are very similar in reproductive biology and fruit form, with one potentially key difference: <u>A</u>. <u>butyracea</u> has endocarp fibers and sunken germination pores protected by these fibers, whereas <u>A</u>. <u>maripa</u> has only a woody endocarp. The fruits of <u>A</u>. <u>butyracea</u> are also slightly larger (4.5 to 8.5 cm long vs. 3.5 to 6.5 cm long; Henderson 1995).

Taxonomy and Taxon-Specific Interactions

Out of 1,500 species of bruchid beetles, only 20 species in four genera (three species of <u>Cayroborus</u>, six species of <u>Caryobruchus</u>, seven species of <u>Pachymerus</u>, and four species of <u>Speciomerus</u>) are palm bruchids (tribe Pachymerini, subfamily Pachymerinae). All are endemic to the New World, and all but one are tropical (Nilsson and Johnson 1993, Delobel et al. 1995, Johnson et al. 1995). On a palm subfamily basis, bruchids are known to associate extensively (many species, many and substantiated records of high infestation rates) with tribes in the Arecoideae and Coryphoideae, and less extensively with a few species in the

Ceroxyloideae, Phytelephantoideae, and Calamoideae (Johnson et al. 1995). Within the Arecoideae, the tribe Cocoeae represents the most intensive association for all Neotropical palms (59% of 22 genera infested). The subtribes Attaleinae (primarily the genus Attalea) and Cocoae (primarily the genus Astrocaryum) have the greatest number of reports of bruchid infestation (Johnson et al. 1995). These are the groups that combine large seeds with thick endocarps.

The most specific association between a palm group and a beetle group is between Attalea palms and two species of beetles, Pachymerus cardo and Speciomerus giganteum. Fifteen out of 24 record for the species Pachymerus cardo are from Attalea palms, as are all of nine records for Speciomerus (Johnson et al. 1995). Both species are widespread, ranging from Central America to the southern Amazon basin.

Ecological Studies

The palm-bruchid system is ideal for study of invertebrate—fruit interactions because eggs, entry holes, larvae, and exit holes are easily counted and endocarps are easily protected from vertebrate predation in the field by wire exclosures. All studies have used some variation of these methods. I evaluate the results of these studies in some detail because misinterpretation of data in some papers has led to a perpetuation of erroneus conclusions in subsequent publications (c.f. Henderson 1995).

Janzen (1971, 1972) described the interactions between
Scheelea buryracea, Speciomerus giganteus, and Pachymerus sp.
in lowland moist forest habitat of Costa Rica. In this
system, beetles lay their eggs on the endocarp only after the
husk and pulp have been almost completely removed by rodents
or by rotting. Egg laying intensity is low, with 2-5 eggs
found per seed after prolonged exposure to oviposition.
Janzen reports a development time of 3 to 5 months; that is,
beetles begin to emerge from the seeds after this amount of
time. Larval infestation rates were greater than 77% for
seeds remaining in the original fruit pile by the parent
tree. Fruit removal by frugivores and endocarp removal by
granivores appears to be low, based on the size of the fruit
piles described as remaining by the parent tree at the end of
the fruiting season. A key observation by Janzen was that by
the time rodents opened the endocarps under the parent tree,
most of them contained full-grown larvae. If the endocarp
contains multiple seeds, they are usually all killed by a
single larva. Janzen also found high larval, pupal, and
adult mortality by an "unknown microbial disease," which
resulted in adult emergence rates much lower than infestation
rates.

Work by Wilson and Janzen (1972) with the same system in
Costa Rica again highlights a long development time for the
larvae ("most are more than half grown" after 4.5 months in
the field). Infestation rate was low (35% of experimental
seeds). Bruchids had difficulty finding endocarps placed

individually rather than in clumps on the forest floor. The
authors suggest that adults emerge from the endocarps after a
rainfall cue at the start of the next palm fruiting season.
Although they timed development and emergence for two beetles
at 66 and 43 days respectively, the authors suggest that the
larvae remain within the endocarps through the dry season
following their laying season, and emerge only at the start
of the next rainy (= fruiting) season. However, they also
suggests that beetles remain in the endocarp in the adult
form, so it is unclear which effect is predominant, or if the
two terms, larvae and beetle, were inadvertently confused in
the paper. In this study, only Speciomerus was present,
whereas in the previous study, trees infested by two species
of beetles were included in the sample of infested seeds.

   Bradford and Smith (1977) compared endocarps from a
small sample of Attalea buryracea trees in Panama and Costa
Rica, both presumably exposed only to predation by
Speciomerus giganteus. They concluded that rodent predation
was high on BCI and low in Costa Rica, whereas the opposite
was true for bruchid predation. This is an erroneous
conclusion, because they classified any rodent-opened
endocarp as preyed on only by rodents, disregarding that fact
that most endocarps opened by rodents probably had a larva in
them, which the rodent would have removed. They do not take
seriously Janzen's suggestion that rodents are encountering
larvae more frequently than endosperm, stating instead that
rodents "possibly" feed on the larvae. They also concluded

that seeds from multiple-seed endocarps had a higher probability of escaping predation than those from single seed endocarps. However, individual trees tend to produce a typical number of seeds per endocarp, and individual trees may also differ strongly in both the degree of bruchid infestation and rodent predation (Chapters 4 and 5). Since Bradford and Smith (1977) only sampled five trees, they could have had a strong tree effect in their study.

Based on differential gnawing patterns at the two sites, the same study also suggested that there is an evolutionarily based correlation between the number of seeds per endocarp and the way in which a single rodent species opens the endocarps. This is based on the assumption that the same rodent species were opening the endocarps at both sites. However, the gnawing patterns they describe could also be interpreted as being caused by different rodent species: on BCI the five trees they sampled appear to have been fed on only by squirrels, whereas in Costa Rica there was also predation by agoutis.

Wright (1983) continued work with the _A_. _butyraceae_-_S_. _giganteus_ system on BCI. He again reports a low ovipostion rate (1-5 eggs, with a rare extreme of 11 eggs after 48 hours of exposure). He found that there was high mortality of either the eggs or the first instar larvae, because only 47 out of 127 endocarps with eggs developed larvae, and many of those without larvae had entry holes that indicated a first instar larvae had at least initiated tunneling through the

endocarp but then failed to develop. He also found that
females could distinguish between endocarps with no eggs and
those with eggs, and preferred to lay on endocarps with no
previous eggs.

In a later study at the same site, Wright (1990)
measured an interval of 5 days from ovipositon to hatching,
and of 6 months from ovipostion to adult emergence. He notes
that some adults, rather than larvae, remain inside the
endocarp until the next wet season. The intensity of
ovipositon, low to start with (0.91 eggs per endocarp),
declined during the fruiting season, and stopped altogether 2
months before the end of the fruiting season. He concludes
that this decline is due to a lack of recruitment into the
beetle population during one fruiting season: beetles have a
long development time and they emerge at the start of each
fruiting season. Like Janzen, he notes that rodents often
consume seeds that were first infested by bruchids, but still
classifies these as rodent-destroyed, even though the bruchid
would undoubtedly have killed the seed in the absence of
rodents.

Working with the Attalea maripa-Pachymerus cardo system
in northern Brazil, Fragoso (1994, 1997) found that seeds
ingested by tapirs (as fruit) and subsequently defecated at
upland latrines had a much higher chance of surviving bruchid
infestation than seeds remaining at the parent tree. This
survival translated to a higher seedling density at latrine
sites than at parent trees or at random locations in the

forest. He also found that bruchids are able to penetrate thicker endocarps than rodents. Like Bradford and Smith (1977), he found that endocarps with multiple seeds were more likely to have at least one seed survive beetle or rodent predation than single-seeded endocarps. However, because single seeded endocarps are thicker than multiple seeded ones, they are more likely to survive attack by white-lipped peccaries, which, unlike rodents and bruchids, cannot penetrate the thickest endocarps. Therefore, white-lipped peccaries could be maintaining selection for thick, single seeded endocarps, which appears to be opposite to the selection pressure for multiple seeded endocarps maintained by bruchids

Astrocaryum-Bruchid System

As for the Attalea-bruchid system, much of the work with Astrocaryum has focused on the role of vertebrate dispersers in protecting seeds from bruchids by burial (Smythe 1989) and on the role of bruchids in distance and density dependent seed predation (Terborgh et al. 1993). Terborgh et al. (1993) documented greater infestation rates near the parent tree than 25 m away for an unknown beetle on Astrocaryum macrocalyx in Peru, when rodents and other vertebrates were excluded.

Delgado et al. (1995) document bruchid predation rates on fruits not affected by vertebrate consumers and find more

rapid oviposition on fruits artificially cleaned of pulp and husk. They report multiple larvae per seed, and rejection of some fruits altogether by ovipositing females. Smythe (1989) found high mortality from bruchids for peeled, unburied Astrocaryum standleyanum seeds on BCI, a result to be expected in light of the protection offered by the husk and pulp (Janzen 1971, Wright 1983, Delgado et al. 1995, Chapter 3).

Bruchid-Invertebrate Interactions

Interactions between bruchids and invertebrate parasites are more rarely recorded than those between vertebrates and bruchids, although parasites can cause significant mortality for bruchid larvae and have seasonal patterns that can affect the evolution of both bruchid beetles and palm phenology (Fragoso and Silvius unpublished data). Quicke and Delobel (1995) described a parasitic wasp species that attacks the late instar larve and pupae of Cayoborus serripes on several species of Astrocaryum palms. Parasitism rates were as high as 20%. The same bruchid species has its eggs parasitized by a trichogrammatid wasp (Delobel et al. 1995), as does Pachymerus cardo on Attalea palms, where egg parasitism rates were as high as 92% (Delobel et al. 1995). Janzen (1971) reports an unknown parasite on Speciomerus giganteus eggs in Costa Rica, as well as an unknown agent of mortality, which he refers to as a pathogen, that kills larvae and pupae.

Given the widespread nature of the parasitism, the high mortality rates recorded, and the probable specificity of the relationship, invertebrate predators and/or parasites on bruchids are likely to be as important in bruchid beetle ecology and evolution as vertebrates. For example, bruchid beetles might chose seeds that offer escape from parasites rather than from rodents.

Summary and Conclusions

The issue of the relationship between fruit availability and frugivore species richness and abundance is undeniably a large one that needs to be tackled in bits and pieces, or by many researchers working together. However, by identifying one subset of frugivores and fruits that show a more or less tight relationship, it may be possible to develop methodologies and theoretical approaches that can then be applied to the larger community of fruits and frugivores.

The review presented here suggests that several Neotropical forest species, namely white-lipped peccaries, tapirs, _Cebus_ monkeys, agoutis, and most importantly squirrels, depend to varying degrees on palm fruit availability. Squirrels, and to a lesser degree capuchin monkeys, are specialized on palm use. The use of palms as a season of scarcity resource (Terborgh 1986a, b) may be restricted to members of the genus _Cebus_. By Terborgh's own

definition, this would then no longer constitute a case of keystone resource use.

In palm species that have ecological and evolutionary interactions with bruchid beetles, it is unclear and unstudied whether frugivores and granivores are feeding on fruit matter or insect matter, and what the effect of these interactions is on palm and frugivore ecology. The _Attalea_-bruchid system is the best understood. Several studies indicate that beetles cause significant mortality for palms, and that both vertebrate predators and invertebrate parasites cause significant mortality for beetles. There is some evidence that seeds dispersed long distances from the parent tree experience reduced beetle predation.

Table 2-1: Results of literature review of palm use by
Neotropical mammals. Latin binomials for palms and mammals
are those used by the original authors; note that all palms
in the genera _Attalea_, _Maximiliana_, _Orbignya_ and _Scheelea_ are
currently placed in the genus _Attalea_. imm = immature, mat =
mature, germ = germinating, fruit = author did not
distinguish between part eaten, endocarp contents = either
endosperm or bruchid larvae or both.

Palm Species	Mammal Species	Part	Site	Ref
Mauritia flexuosa	_Mazama americana_	pulp	Maracá, Brazil	17
	Tayassu pecari	preripe seed, germ, seed		19
	Tayassu tajacu	germ. seed		19
	Tapirus terrestris	pulp		18
	Ateles belzebuth	mat pulp	Maracá, Brazil	33
	Mazama americana		N.E. Peru	6
	Mazama gouazoubira			6
	Tayassu tajacu			6
	Tayassu pecari			6
	Tapirus terrestris			6
	Nectomys squamipes	embryo from seed, pulp, discards endo sperm	Mato Grosso, Brazil	40
	Oxymycteris roberti	pulp, caches seeds		40
	Oligorysomys sp.	pulp, seed coat		40
	Didelphis albiventris	pulp		40

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
	Tapirus terrestris	pulp		40
	Agouti paca	pulp seed (holds with fore paws)		40
	Chrysochyon brachyurus	pulp		40
	Dasyprocta fuliginosa.		N.E. Peru	1
	Small rodents			1
	Agouti paca			1
	Eira barbara			1
	Tapirus terrestris			1
	Mazama americana			1
	marsupials			1
	edentates			1
	Marmosops noctivagus		N.E. Peru	52
	Marmosops sp.			52
	Nectomys squamipes			52
	Oecomys trinitatis			52
	Oryzomys sp.			52
	Oryzomys yunganus			52
	Proechimys sp.			52
	Proechimys steereei			52
Attalea maripa	*Sciurus spadiceus*	imm. seed mat. pulp	Rio Urucu, Brazil	38
	Ateles belzebuth	mature pulp	Bolivar, Vene-zuela	11
	Cebus apella	mat pulp	Amazonas Brazil	47
	Odocoileus virginianus	pulp	Maracá, Brazil	17

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
	Tayassu tajacu	pulp		43
	Tayassu pecari	pulp endocarp contents		17, 42
	Ateles belzebuth	mat pulp	Maracá, Brazil	33
	Alouatta seniculus	pulp		43
	Saimiri sciurus	pulp		43
	Sciurus igniventris	seed		42
	Dasyprocta agouti	pulp seed		42, 43
	Dasyprocta punctata		French Guiana	28
	Sciurus aestuans			28
	Ateles belzebuth	fruit	Bolivar, Venezuela	11
Attalea regia	*Cebus albifrons*	pulp seed	Eastern Colombia	14
	Echimys armatus	pulp	French Guiana	12
	Philander opossum	pulp		12
	Didelphis marusupialis	pulp		12
	Sciurus aestuans	seed		12
	Dasyprocta agouti	seed		12
	Agouti paca	pulp		12
	Small rodents	pulp		12
Attalea phalerata	*Tapirus terrestris*	pulp	Beni, Bolivia	27
Scheelea sp.	*Saimiri sciurus*	seed	Cocha Cashu, Peru	49
	Cebus apella	seed		49
	Cebus albifrons	seed		49
	Sciurus spadiceus	seed		49
Scheelea sp.	*Sciurus igniventris*	seed	Western Amazonia	15
Scheelea sp.	*Ateles paniscus chamek*		Cocha Cashu, Peru	48

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
Scheelea sp.	*Tapirus terrestris*		S. E. Peru	6
Scheelea rostrata	*Sciurus variegatoides*	pulp seed	Costa Rica	7
	Agouti paca	pulp seed		7
	Dasyprocta punctata	pulp seed		7
Scheelea zonensis	*Nasua narica*	pulp	BCI	55
	Cebus capucinus	pulp		34
	Agouti paca	pulp		7
	Dasyprocta punctata	seed pulp		45
	Proechimys semispinosus	seed pulp		7
	Sciurus granatensis	seed pulp		21, 7
	Sciurus gerradi			55
Scheelea attaloides	*Cebus apella*	pulp	Colombia	26
Orbignya martiana	*Agouti paca*	pulp	Maranhão Brazil	3
	Dasyprocta punctata	pulp		3
	Coendu prehensilis	pulp		3
	Coendu sp.	pulp		3
	Proechimys longicaudata	pulp		3
	Mesomys hispidus	pulp		3
	Tayassu pecari	pulp		3
	Tayassu tajacu	pulp		3
	Aotus trikingatus	imm. seed		3
	Cebus apella	imm. seed		3
Orbignya phalerata	*Chiropotes sp.*	pulp	Pará, Brazil	5
Orbignya cohune	*Cebus capucinus*	seed	Honduras	9
Astrocaryum murumuru	*Sciurus spadiceus*	imm seed	Rio Urucu, Brazil	36, 37
	Cebus apella	pulp	Cocha Cashu, Peru	13
	Sciurus spp.	seed		13

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
	Dasyprocta variegata	seed		13
	Proechimys spp.	seed		13
	Oryzomis spp.	seed		13
	Tayassu pecari	seed		13
Astrocaryum sp.	*Mazama americana*	pulp	N.E. Peru	6
	Tayassu tajacu	seed		6
	Tayassu pecari	seed		6
	Tapirus terrestris			6
Astrocaryum aculeatum	*Ateles belzebuth*	imm pulp	Maracá, Brazil	33
	Tayassu pecari	seed		17
	Tayassu tajacu	pulp		43
	Tapirus terrestris	pulp		43
	Cebus nigrivitatus	imm pulp		43
	Dayprocta agouti	pulp seed		43
	Scirus igniventris	fruit		43
Astrocaryum sp. (=murumuru?)	*Cebus capucinus*	seed	Cocha Cashu, Peru	49
	Cebus albifrons	seed		49
	Sciurus spadiceus	seed		49
	Tayassu sp.	seed		49
Astrocaryum chambira	*Cebus apella*	imm seed	La Macarena Colombia	26
	Ateles belzebuth	imm seed		26
	Lagothrix lagothrica	imm seed		26
	Cebus apella	"nut"	Colombia	46
Astrocaryum mexicanum	*Sciurus aureogaster*	seed	Mexico	39
	Sciurus deppei	seed		39
	Heteromys desmarestianus	seed	Belize	8
Astrocaryum standleyanum	*Nasua narica*	pulp imm fruit	BCI	55

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
	Agouti paca	pulp		44, 45
	Cebus capucinus	pulp		34
	Ateles geoffroyi	pulp		24
	Dasyprocta punctata	pulp		45
	Sciurus granatensis	seed		21
	Didelphis marsupialis	pulp		44
	Philander opossum	pulp		44
	Caluromys derbianus	pulp		44
	Tayassu pecari	seed		44
	Tayassu tajacu	seed		44
	Heteromys desmarestianus	seed		44
	Proechimys semispinosus	seed		44, 2, 25
	Tapirus bairdii			55
Astrocaryum vulgare	*Philander opossum*	pulp	French Guiana	12
	Caluromys philander	pulp		12
	Dasyprocta punctata	seed		12
	Coendu prehensilis	pulp		12
	Agouti paca	pulp		12
	small rodents	pulp		12
	Sciurus aestuans	seed		12
Astrocaryum paramaca	*Sciurus aestuans*		French Guiana	28
	Proechimys cuvieri			28
Astrocaryum sciophilum	*Sciurus aestuans*		French Guiana	28
	Myoprocta exilis			28
Astrocaryum sp.	*Proechimys semispinosus*		Cocha Cashu, Peru	15
Astrocaryum sp	*Sciurus spadiceus*	seed	Western Amazonia	15

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
	Sciurus igniventris	seed		15
Chamaedorea tepejilote	*Heteromys desmarestianus*	seed	Mexico	35
	Agouti paca			55
Socratea exorrhiza	*Ateles belzebuth*		Colombia	31
	Ateles belzebut	fruit	Bolivar, Vene-zuela	11
	small rodents	seed	Maracá, Brazil	43
	Tayassu pecari	seed	Maracá, Brazil	43
	Artibeus jamaicensis	fruit	Amazonia French Guiana, Trinidad	55, 12
	Artibeus lituratus		Amazonia French Guiana	55, 12
Socratea durissima	*Dasyprocta punctata*		BCI	45
	Sciurus granatensis			21
	Cebus capucinus	pulp		34
	Ateles geoffroyi	mat pulp		24
	Alouatta palliata	pulp		32
	Proechymis semispinosus			55
	Myoprocta exilis		French Guiana	12
	Heteromys desmarestianus	seed	Costa Rica	66
Socratea sp.	*Tayassu tajacu*		Cocha Cashu Peru	29
	Tayassu pecari			29
Socratea sp.	*Ateles paniscus chamek*	pulp	Cocha Cashu Peru	48
Socratea elegans	*Cebus apella*	imm. seed	Colombia	26
	Ateles belzebuth	imm. seed	Colombia	26

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
Iriartea ventricosa	*Ateles belzebuth*		Colombia	31
	Tayassu pecari	seed ?pulp	Cocha Cashu, Peru	30
	Cebus apella			49
	Saguinus imperator			49
	Saguinus fuscicolis			49
	Callicebus moloch			49
	Ateles paniscus chamek	pulp seed		48
	Proechimys semispinosus	seed		15
Iriartea sp.	*Mazama americana*	seed pulp	N.E. Peru	6
	Mazama gouazoubira	seed pulp		6
	Tayassu tajacu	fruit		6
	Tayssu pecari	fruit	·	6
Wettinia maynensis	*Saguinus sp.*			55
Euterpe sp.	*Ateles belzebuth*		Colombia	31
Euterpe sp.	*Ateles paniscus*	pulp	Cocha Cashu, Peru	48
Euterpe precatoria	*Cebus apella*	mat pulp	Colombia	26
	Ateles belzebuth	fruit	Maracá, Brazil	43
Oenocarus bacaba	*Ateles belzebuth*	mat.fruit	Maracá, Brazil	33
Oenocarpus mapora	*Cebus apella*	imm seed, mat pulp	Colombia	26
Oenocarpus panamus	*Sciurus granatensis*		BCI	23
	Cebus capucinus			34
Oenocarpus sp.	*Ateles belzebuth*		Colombia	31
Jessenia bataua	*Cebus apella*	imm seed	Rio Urucu, Brazil	37
	Cebus albifrons			37

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
	Pithecia albicans	imm seeds, mat pulp		37
	Lagothrix lagrothrica cana			37
	Pithecia sp.	mat pulp	Pará, Brazil	5
	Tayassu tajacu	pulp	N.E. Peru	6
	Tayassu pecari	pulp		6
	Mazama americana	pulp		6
	Tapirus terrestris	pulp		6
	Pithecia monachus			55
	Cebus albifrons	pulp seed	Eastern Colombia	14
	Cebus apella	imm seed mat seed mat pulp	Colombia	26
	Ateles belzebuth	imm seed mat seed mat pulp		26
	Ateles belzebuth	fruit	Bolivar, Venezuela	11
	Cebus nigrivitatus		Amazonia	28
	Sciurus aestuans		French guiana	28
Roystonea oleracea	*Artibeus lituratus*	fruit	Trinidad	55
Syiagrus orinocensis	*Cebus albifrons*	pulp seed	Eastern Colombia	14
Syagrus romanzonffiana	*Cebus apella*	mat pulp	Campinas Brazil	20
	Alouatta fusca	mat pulp		20
	Sciurus ingrami	imm seed old seed		20
Acrocomia sp.	*Dasyprocta sp.*		Central Brazil	55
	Cerdocyon thous			55

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
Acrocomia aculeata	*Didelphis albiventris*		dry upland habitat, Brazil	55
	Nectomys squamipes			55
	Cebus apella			55
	Agouti paca			55
	Euphractes sexcintus			55
	Dasyprocta sp.			55
Acrocomia vinifera	*Sigmodon hispidus*	pulp	Costa Rica	4
	Tayassu tajacu	pulp seed		4
Bactris barronis	*Sciurus granatensis*		BCI	21
Bactris sp.	*Mazama americana*		N.E. Peru	6
Bactris sp.	*Artibeus jamaicensis triniatus*	fruit	Trinidad	22
	Altibeus lituratus palmarum	fruit		22
Bactris sp.	*Ceus albifrons*	pulp seed	Eastern Colombia	14
Bactris gassipaes	*Heteromys desmarestianus*	pulp	Costa Rica	53
	Hoplomys gymnurus	pulp		53
	Dasyprocta punctata	pulp		53
Bactris sp.	*Saguinus fuscicollis*	mat fruit	Rio Urucu, Brazil	36
Bactris sp.	*Cebus capucinus*	fruit	Honduras	9
Paurotis wrightii	*Cebus capucinus*	fruit	Honduras	9
Desmoncus isthmius	*Cebus capucinus*	pulp	BCI	34
Welfia georgii	*Potos flavus*		Costa Rica	54
	Sciurus sp.			54
	Ceus capucinus			54
	Dasyprocta punctata			54

Table 2-1, continued

Palm Species	Mammal Species	Part	Site	Ref
	Heteromys desmarestianus			54
	Haplomys gymnurus			54
	Proechymis semispinous			54
	Agouti paca?			54
	Tayassu pecari?			54
Phytlephas sp.	*Dasyprocta sp.*			55
Ammandra sp.	*Dasyprocta sp.*			55
Washingtonia filifera	*Canis lastrans*	pulp	Sonora	10
	Urocyon cineroargentatus	pulp		10
Copernicia tectorum	*Cebus nigrivitatus*	imm fruit germ seeds endocarp contents	Llanos, Vene-zuela	41
Areca lutescens	*Phyllostomatidae*			22
Coccothrinax sp.	*Phyllostomatidae*			22

1-Allen 1997; 2-Adler 1995; 3-Anderson 1983; 4-Baker 1983; 5-Bobadilla, pers. comm.; 6-Bodmer 1989; 7-Bradford and Smith 1977; 8-Brewer and Rejmanek 1998; 9-Buckley 1983; 10-Bullock 1980; 11-Castellanos and Chanin 1996; 12-Charles Dominique et al. 1981; 13-Cintra and Horna 1997; 14-Defler 1979; 15-Emmons 1982; 16-Fleming 1974; 17-Fragoso, pers. comm; 18-Fragoso 1997; 19-Fragoso 1994; 20-Galeti et al. 1992; 21-Glanz et al. 1996; 22-Gardner 1977; 23-Heany and Thorington 1978 24-Hladik and Hladik 1969; 25-Hoch and Adler 1997; 26-Izawa 1979; 27-Quiroga 1997; 28-Kahn and de Granville 1992; 29-Kiltie 1981; 30-Kiltie and Terborgh 1983; 31-Klein 1972; 32-Milton 1980; 33-Nuñes 1992; 34-Oppenheimer 1996; 35-Oyama 1991; 36-Peres 1993b; 37-Peres 1994a; 38-Peres 1994b; 39-Piñero et al. 1984; 40-Prada 1994; 41-Robinson 1986; 42-Silvius, this study; 43-Silvius pers. obs.; 44-Smythe 1989; 45-Smythe et al. 1996; 46-Spironelo 1991; 47-Struhsaker and Leland 1977; 48-Symington 1987; 49-Terborgh 1977; 50-Terborgh 1986a; 51-Terborgh 1986b; 52-Valqui unpublished data; 53-Vandermeer 1983; 54-Vandermeer et al. 1979; 55-Zona and Henderson 1989.

Table 2-2. Palm-eating mammals for which the percent composition of the diet has been estimated.

Mammal Species	Palm Species	% of total or annual diet	Highest monthly %	Reference
Cebus apella	*Jessenia (Oenocarpus) bataua and Attalea maripa primarily, and some Oenocarpus bacaba, Astrocaryum mumbaca, Mauritia flexuosa, and Syagrus inajai (data combined)*	17.6	53	Spironelo 1991 1-year study
	Jessenia bataua		24.5	
	Attalea maripa		28.7	
	Astrocaryum mumbaca		3.5	
Ateles belzebuth belzebuth	*Attalea maripa*	1.23	10.1	Nuñes 1992 2-year study
	Astrocaryum aculeatum	0.18		
	Oenocarpus bacaba	0.09		
	Mauritia flexuosa	0.09		
Mazama americana	*Astrocaryum sp.*	3.4 (5)		Bodmer 1989*, 15 month study
	Bactris sp.	9.1		
	Euterpe sp.	43.6 (1)		
	Iriartea sp.	34.4 (2)		
	Jessenia (Oenocarpus) bataua	1.1		
	Mauritia flexuosa	9.1		
Mazama gouazoubira	*Euterpe sp.*	48.0 (1)		

Table 2-2, continued

Mammal Species	Palm Species	% of total or annual diet	Highest monthly %	Reference
	Iriartea sp.	36.0 (2)		
	Mauritia flexuosa	8.0		
Tayassu tajacu	*Astrocaryum sp.*	45.3 (3)		
	Euterpe sp.	7.5		
	Iriartea sp.	27.7		
	Jessenia (Oenocarpus) bataua	46.2 (2)		
	Mauritia flexuosa	11.7		
Tayassu pecari	*Astrocaryum sp.*	47.7		
	Euterpe sp.	15.9		
	Iriartea sp.	75.0 (1)		
	Jessenia (Oenocarpus) bataua	59.0 (2)		
	Mauritia flexuosa	45.0		
Tapirus terrestris	*Astrocaryum sp.*	5.3		
	Jessenia (Oenocarpus) bataua	23.7 (2)		
	Mauritia flexuosa	76.3 (1)		
	Attalea sp.	13.2		
Dasyprocta punctata	*Astrocaryum standleyanum*	22.7		Smythe et al. 1996, 1-year study, 326 feeding observations
	Attalea butyracea	11.04		
	Oenocarpus panamus	0.31		
	Socratea durissima	0.31		

Table 2-2, continued

Mammal Species	Palm Species	% of total or annual diet	Highest monthly %	Reference
Agouti paca	*Astrocaryum standleyanum*	6.7		Smythe et al. 1986, 1-year study, 15 feeding observations
Sciurus granatensis	*Astrocaryum standleyanum*	20.92		Glanz et al. 1986, 2-year study
	Bactris barronis	0.05		
	Bactris major	0.05		
	Oenocarpus panamus	0.68		
	Attalea butyracea	24.62		
	Socratea durissima	0.05		
Cebus capucinus	*Attalea cohune*	rank 1	14.3-58.2 May-October	Buckley 1983, 17 month study
Sciurus ingrami	*Syagrus romanzof-fiana*	49.0		Galetti et al. 1992
Cebus apella	*Syagrus romanzof-fiana*	2.16		
Alouatta fusca	*Syagrus romanzof-fiana*	0.25		
Ateles belzebuth	*Euterpe sp.*	1.0	61.0	Klein 1972, 1-year study
	Socratea exorrhiza	1+	1+	
	Iriartea ventricosa	2.0	23.0	
	Oenocarpus sp.	1+	22.0	
Saguinus fuscicolis	*Bactris sp.*	0.03		Peres 1993a, 20-month study
Pithecia albicans	*Mauritia flexuosa*	2.3		Peres 1993b, 20-month study

Table 2-2, continued

Mammal Species	Palm Species	% of total or annual diet	Highest monthly %	Reference
Ateles paniscus	Palmae	0.9		Roosmalen 1980; 2-year study
	Euterpe oleracea	0.3		
	Attalea regia (?=maripa)	0.3		
	Oenocarpus bacaba	0.2		
	Euterpe oleracea	0.05		
Sciurus spadiceus, Sciurus igniventris	Palmae	98.0 %		Emmons 1984
Sciurus granatensis	Astrocaryum standleyanum	9.0	22	Heany and Thorington 1978; 4 months, rainy and dry seasons
	Oenocarpus panamus	1	7	
	Attalea butyracea	27	86	
Cebus apella	Palmae (5 sp)		64 from May to July	Terborgh 1983, 12-month study
Cebus albifrons	Palmae (5 sp)		56 from May to July	
Saimiri sciurus	Palmae (3 sp)		15 from May to July	
Saguinus imperator	Palmae (1 sp)		< 1 from May to July	
Saguinus fuscicolis	Palmae (1 sp)		< 1 from May to July	

* In this study, % is the percent of stomachs in which the food item occurred, while in all the other studies, it is the percent of feeding observations, either instantaneous or over a defined sampling period, in which that food item was eaten. For clarification, in Bodmer's study I give in parentheses, next to the percentage, the rank in the diet based on the percent of total dry weight of all stomach contents combined, if the palm ranks between first, second or third in importance in the diet.

Table 2-3. Revisions to palm and bruchid taxa referred to in the text.

FORMER NAME	CURRENT NAME	REFERENCES
Palms		
Maximiliana maripa	*Attalea maripa*	Fragoso 1994, 1997
Scheelea zonensis	*Attalea butyracea*	Bradford and Smith 1977, Wright 1983, Wright 1990, Forget 1994
Scheelea rostrata	*Attalea butyracea*	Janzen 1971, Janzen and Wilson 1972, Bradford and Smith 1977
Orbignya phalerata	*Attalea speciosa*	Anderson 1983, Anderson et al. 1991
Bruchids		
Caryobruchus bucksii	*Speciomerus giganteus*	Janzen 1971, Janzen and Wilson 1972
Unidentified	*Pachymerus cardo*	Fragoso 1994

CHAPTER 3
PULP HANDLING BY MAMMALIAN FRUIT-EATERS AFFECTS PALM SEED
PREDATION BY BRUCHID BEETLES

Introduction

Studies of frugivory systems (a fleshy-fruited plant
population and its consumer set, Howe 1993) to date have
focused primarily on the interactions between plants and
vertebrate fruit-eaters (Estrada and Fleming 1986, Fleming
and Estrada 1993). This bias has resulted in a dominance of
vertebrate-based evolutionary scenarios for both fruit trait
evolution and plant demography. Thus fruit traits are
interpreted as evolving in response to the need to attract
pulp eaters that disperse seeds to safe sites. A limited
group or researchers, led by the early theoretical work of
Herrera (1982) and Janzen (1977), has focused on the
interactions between fruits and invertebrates, including both
seed eaters and pulp eaters. In this study I focus on
interactions between pulp, insects, and vertebrates, leaving
discussion of interactions involving seeds for the next
chapter.

Several studies show that invertebrate pulp consumers or
the fungal spores they introduce into pulp can degrade pulp
and make it unattractive to vertebrate pulp eaters that might

otherwise disperse the seeds (Jordano 1987, Borowicz 1988, Krishik et al. 1989, Buchloz and Levey 1990, Sallabanks and Courtney 1992, Cipollini and Stiles 1993). In other cases, invertebrates may enhance pulp quality for the vertebrate disperser/pulp eaters by providing protein, lipids, and other nutrients (Redford et al. 1984, Piper 1986, Valburg 1992a,b). The opposite effect, alteration of fruit quality by vertebrate pulp consumers for invertebrate fruit consumers, has seldom been examined, although it has been noted that some insect species preferentially lay their eggs into damaged areas of the pulp (Sallabanks and Courtney 1992). In such a situation, presumed dispersers who scar the pulp could have a negative effect on seed survival by increasing the likelihood of infestation by invertebrate seed eaters.

Due to variation in body size and behavior, different species of fruit-eaters handle pulp in distinct ways, and remove varying amounts of pulp from the fruits they handle. Differences in the amount and pattern of pulp removal could affect seed predation rates by insects and ultimately plant demography. In the Neotropics, a diverse array of consumers eat the fruits of arborescent palms: primates, carnivores, rodents, ungulates, and marsupials among the mammals, psittacines, falconiformes, and icterids among the birds, and tortoises among the reptiles (Chapter 2). Several Neotropical palm species are also parasitized by about 20 species of bruchid beetles (Chapter 2). One of the most specific and widespread relationships is that between palms

in the genus _Attalea_ (including _Maximiliana_, _Orbygnia_, and _Scheelea_; Henderson 1995) and the beetles _Pachymerus cardo_ and _Speciomerus giganteus_. Interactions among these taxa have been documented from Costa Rica to Bolivia (Fragoso 1997b, Quiroga 1997, Johnson et al. 1995, Janzen 1971, Wilson and Janzen 1972).

In the palm-bruchid system, interactions between bruchids, vertebrate seed eaters, and nut walls (endocarps) have been examined in some detail (Fragoso 1994, Wright 1983, 1991, Bradford and Smith 1977). The fruit husk (exocarp) and the pulp (mesocarp), however, are the first barriers bruchids encounter when attacking a seed, long before they reach the endocarp. Both affect the bruchids' ability to reach a seed. Janzen and Wright (Janzen 1970, Wright 1983, 1990) noted that bruchids do not lay eggs on endocarps of _Attalea butyracea_ in Central America until the husk and most of the pulp has been removed by vertebrates or fungus. The same was true for an _Astrocaryum_ palm in Peru whose pulp was experimentally removed (Delgado et al. 1997). This indicates that pulp itself acts as a deterrent to oviposition.

Several researchers have suggested that pulp chemicals in plant families other than the Palmae may deter feeding by insects (reviewed in Cipollini and Levey 1997), but there is little consideration in the literature of pulp as a physical deterrent for seed-eating insects. The physical properties of pulp, however, including consistency and presence of mucilage or lipids, could impede pulp mining by insects. Extremely

thick pulp could also increase mortality of larvae mining their way into the seeds. Traits associated with the attraction of seed dispersing mammals could thus also function as repellents to insects. Because pulp has evolved many times in the Angiosperm lineage, in some of these cases pulp could be evolutionarily molded by selection by insect seed predators as well as by dispersers. Given the extremely high rates of mortality caused by Coleoptera (especially Bruchidae and Curculionidae, Janzen 1982a,b, 1983, Herrera 1989, Sallabanks and Courtney 1992) in the tropics, selection for deterrence of beetle larvae should be strong.

On Maracá Island Ecological Reserve, in the northern Brazilian Amazon, high rates of bruchid predation by Pachymerus cardo have been documented for the common arborescent palm Attalea maripa (= Maximiliana maripa) (Fragoso 1994, 1997b). The present study experimentally examines the effect of differential pulp handling by vertebrate consumers on a) pulp-dependent egg-laying choices by bruchid beetles that parasitize the seeds, and b) subsequent survival rate of seeds that received differing numbers of eggs in response to different pulp characteristics.

Study Area and Species

Study Area

Maracá Island Ecological Reserve is a 1,100 km^2 riverine island located on the forest side of the forest-savanna boundary in the northern Brazilian state of Roraima. The study site terrain is flat and low (elevation ranges from 110-160 meters above sea level.) The sandy soils are derived from quartz-biotite schists, quartz-feldspar gneisses, and tonalitic granites (Thompson et al. 1992).

Rainfall records on the eastern end of the island show variation of between 1750 and 2,300 mm annually; during El Niño Southern Oscillation events, rainfall decreases markedly across the state. The wet season is between May and September, the dry season between October and April, with rains starting either in early or late April. The heaviest individual rains tend to fall in the dry season.

Study Species

Attalea maripa is a canopy to subcanopy arborescent palm very common on the eastern end of Maracá island (Milliken and Ratter 1989). In the terra firme forest where this study took place, it occurs in dense aggregations (mean 20.2 trees per quarter hectare, range 12-32 trees; Fragoso 1997b). It reaches its highest densities and reproductive output at

ecotones between the forest and either savannas, wetlands or rivers (Chapter 4), and occurs at low densities or singly in the forest interior. Individual infloresences can be bisexual or male, and between one and three fruit bunches develop simultaneously or over the course of a six month fruiting season (April - September). Each fruit bunch can have between a few hundred and more than 3,000 fruits (two average-sized pre-ripe fruit bunches contained 1,183 and 2,455 fruits, respectively). Although a large proportion of reproductive age trees produce flowers, a much lower proportion develops fruits each year (pers. obs., Fragoso unpublished data).

Individual fruits range from 3 to 6 cm in length, and are roughly egg shaped, with a narrow tip and broad base. The husk is about one mm thick, dry and resistant to tearing. The mesocarp is one centimeter thick, dense and slippery, with fibers near the endocarp but not on the outside. It is slightly sweet, soapy and astringent to the human taste, and clings to the mouth parts. Color ranges from pale yellow to bright orange among different trees, but is consistent within one tree. Endocarp thickness ranges from 1.5 to 6.5 mm. Each endocarp can contain one, two, or three seeds, but one seed is most common (Fragoso 1994).

Fruits drop intact to the ground when they are ripe, but many are knocked down (prior to abscission) by primates and bird, often with the pulp only partly removed. The pulp is eaten by brocket deer (_Mazama_ spp.), white-tailed deer

(_Odocoileus virginianus_), collared and white-lipped peccaries (_Tayassu tajacu_ and _T. pecari_), agoutis (_Dasyprocta agouti_), pacas (_Agouti paca_), tapir (_Tapirus terrestris_), capuchin (_Cebus nigrivitatus_, _C. apella_), squirrel (_Saimiri sciureus_), howler (_Allouata seniculus_), and spider monkeys (_Ateles belzebuth_), Amazon parrots (_Amazona_ spp.), macaws (_Ara_ spp.), fruit caracaras (_Daptrius_ sp.), and oropendulas (_Gymnostinops_ sp.). Among the invertebrates, members of the Coleoptera, Diptera and Orthoptera feed on the new pulp, and Dipterans and Dermapterans lay eggs in the pulp. The mature endosperm is eaten by bruchid beetles, squirrels (_Sciurus igniventris_), agoutis (_Dasyprocta agouti_), unidentified small rodent(s), and white-lipped peccaries (_Tayassu pecari_). The immature endosperm is occasionally eaten by an unidentified arboreal consumer that is able to penetrate the immature endocarp.

The bruchid beetle _Pachymerus cardo_ occurs from Costa Rica to Bolivia. It most frequently parasitizes seeds of the genus _Attalea_, but has also been found on _Acrocomia_, _Aiphanes_, _Areca_, _Bactris_, _Copernicia_, _Syagrus_, and _Elaeis_ (Johnson et al. 1995). Like most bruchid beetles, it is nocturnal. Its adult biology is unstudied, and it is presumed to feed on pollen and nectar, though not necessarily of the same palm parasitized by its larvae.

On Maracá, adult beetles lay eggs on the pulp or endocarp of the fruits once they have fallen to the ground (though at nearby open pasture sites they sometimes parasitize intact fruits on the tree; Fragoso and Silvius

unpublished data). After seven to 10 days the first instar
larvae emerge from the eggs and drill through the endocarp
into the seed. Development rates are variable: larvae feed
on the endosperm and remain within the endocarp for a period
of between two to nine months, and possibly longer, before
pupating. Adults emerge from the endocarp at all times of
the year. Both seed size and moisture availability during
development appear to influence the size of the larvae and of
the emerging beetle.

Although many first instar larvae enter the endocarp,
only one larvae develops per endosperm. In the case of
multiple-seeded fruits, two or three larvae can develop in an
endocarp, but usually a single larva eats all of the seeds.

Bruchid eggs in this study were parasitized by an
unidentified insect, and were also attacked by small ants.
Late instar bruchid larvae are parasitized by a wasp
(Hymenoptera: Braconidae) and by another, unidentified
insect.

Beetles in this study were identified by Dr. J.
Kingsolver of the Division of Plant Industry, Florida
Agriculture and Consumer Services. Only P. cardo was found
during this study, but a few individuals of Speciomerus
giganteus were found in Attalea seeds at a forest site 10
kilometers away.

Methods

One 2-part experiment with 1,400 fruits and one single experiment with 100 fruits were carried out from June to December 1996.

Part I: Oviposition Preferences on Fruits with Different Amounts of Pulp

The first part of the experiment tested the hypothesis that the amount of pulp remaining on an endocarp affects the quality of oviposition sites on the endocarp. Female bruchids should lay eggs preferentially on the higher quality "fruit types" and this preference can be measured by counting the number of eggs laid.

Of several conditions in which fruits were found under the parent tree, five "types" were chosen as the most representative and distinct for this experiment. These are described below in order of increasing pulp removal, along with the method by which they were procured for the experiment.

1) Intact husk fruits. Fruits that fell to the ground naturally or were dropped by primates without being opened. For the experiment, these were easily obtained by collecting intact ripe fruits from the ground or tree.

2) Intact pulp fruits. Fruits whose husk was removed by primates, but either rejected or accidentally dropped before pulp removal. Capuchin monkeys often removed only a thin layer of pulp along with the husk, and fruits eaten in this way resembled intact pulp fruits. Howler monkeys also removed only thin layers of pulp, but tended to leave narrow tooth marks in the pulp, whereas capuchins left wider, shallower scrapes. Spider monkeys, which swallow the fruits after squeezing them from the husk, dropped many intact, husk-free fruits. For the experiment, Intact Pulp fruits were obtained by peeling the husk away from intact fruits, taking care not to gash the pulp.

3) Gashed fruits. Squirrel monkeys, macaws, and several ungulate species removed the pulp in deep gashes that exposed the endocarp but left strips of endocarp surrounded by a thick bed of pulp. For the experiments, I artificially gashed intact pulp fruits by biting at the pulp and tearing it away in four locations per fruit.

4) Rodent fruits. Agoutis, and presumably pacas, removed the pulp in a corncob pattern, squeezing most of the juicy pulp out from the fibers but leaving a layer of moist fibers over the endocarp. Because Attalea pulp is a favored fruit of agoutis, many fresh (few hours after being eaten) rodent-chewed fruits could be obtained from the forest floor for the experiments. Fresh fruits were recognizable because the

remaining pulp was still moist, sticky, and shiny, retained
its original color and odor, and the tooth marks were clearly
visible in the stretched-up fibers. Older rodent eaten
fruits began to ferment within a few hours of use, causing
their color, odor, and fiber pattern to change. On several
occasions I also set out intact fruits in areas were I knew
agoutis were actively feeding on <u>Attalea</u> fruits, and
collected the eaten fruits later in the day.

5) Bare endocarps: Ungulates occasionally removed all the
pulp and fiber from endocarps (e.g., those endocarps spat out
by tapirs). Fruits of any of the above types that were left
to rot under parent trees, and seeds defecated by spider
monkeys or tapirs, also had little or no fiber on them. Bare
endocarps were obtained by scraping away most of the pulp
from intact fruits with a knife, then soaking them in water
for a few hours or overnight to remove the remaining fiber.

All fruits were collected and prepared the day before
each experimental set up was placed in the forest, then kept
in a refrigerator until the experiment was set up in the
afternoon of the following day. If fruits were collected
from several different trees, they were mixed together and
then placed haphazardly into the different fruit categories.
Because fruit size varies markedly among trees, when
different sizes had to be used in a single set up, an attempt
was made to partition fruit sizes equally among fruit types.
All endocarps were measured after the experiment was complete

and One-Factor ANOVA's were used to test for differences in size among fruit types within each season. There were no significant differences in endocarp size in any season ($F = 0.63$, $p = 0.64$ in June; $F = 2.17$, $p = 0.0716$ in July; and $F = 1.77$, $p = 0.13$ in Septemer).

Fruits were protected from vertebrate pulp and seed eaters by galvanized wire exclosures ("chicken wire" with mesh size 1.5 x 1.5 cm) 5 cm in height and approximately 23 cm on four sides, with a closed top. These cages were effective in deterring vertebrates from feeding or stepping on the fruits, and provided protection from falling debris. Five exclosures, one for each fruit type and each containing ten fruits, were placed in a star pattern (with one corner touching) at the edge of a fruiting tree's natural seed shadow (1-4 meters from the base of the three) to prevent disturbance from falling fruits (Fig. 3-1). All fruiting trees used had been dropping fruit for at least several days, and had at least 100 naturally fallen fruits in the fruit pile. Fruits were separated by 1-3 cm from each other within each exclosure and were set directly on the natural leaf litter (in preliminary trials with cleared ground, soil disturbance attracted ants, which covered the fruits with dirt).

The experiment was repeated three times at different stages of the palm fruiting season: 10 set ups in June (early peak), 10 in July (late peak), and 8 in September (tail-end of season). Thus the sample size for each fruit type in each

season was 10 replicates (8 in September) of 10 fruits each (Fig. 3-1). Because few trees at the same fruiting stage were available at any one time, trees were used as they became available. Sometimes several trees could be set on one day, and sometimes only one. All trees were within 1.5 km of each other, and had several other Attalea trees within 50 meters.

All fruits were checked twice after each experiment was set up: once the on morning following the set up, so that beetles had only one night to lay eggs, and again 7 days later, when the beetles had seven nights for egg laying. For the first five set ups in June, an attempt was made to count eggs after 14 nights of exposure, but was abandoned because hatching larvae and eggs slid off easily from the rotting pulp when handled. Only the eggs on Intact Pulp fruits could be successfully counted after 14 days. At each count, endocarps were picked up, all eggs counted, and the endocarps returned to their original position. For endocarps with a lot of pulp, the entire fruit was palpated carefully to feel for eggs hidden in the pulp. On Intact Husk fruits, the husk was not lifted up after it started to rot, to avoid exposing more pulp to beetles, and therefore some eggs may have been missed. Eggs on the other fruits were easy to locate.

Intact Husks, but not the other fruit types, were examined weekly for up to nine weeks following set up. The condition of the husk, the number of eggs, and the location of the eggs (on husk or pulp) were noted.

Data Analysis, Part I

Because of the large number of zeros for non-preferred
fruit types, the data were summarized as the mean number of
eggs per seed for each tree x seed type combination, yielding
10 seed type replicates in June and July, and 8 in September.
Because the patterns in seed preference were the same for the
first and second counts, even though the total number of eggs
was lower after one night, only the second count was
analyzed.

Because Intact Husk fruits received no eggs by the
second egg count, data on this fruit type were analyzed
separately from data on the other four fruit types. Timing
of oviposition on Intact Husk fruits is described in detail,
as this is the main factor bearing on seed survival for this
fruit type.

The number of eggs per fruit within each of the
remaining four fruit types was not normally distributed, and
variance was greater in June than in July and September. The
data were normalized by $\log(1 + x)$ transformation, and
analyzed with a two factor ANOVA, with fruit type and season
as factors. Post-hoc comparisons were made with Scheffe F
tests at the alpha = 0.01 level to detect significant
differences between pairs of seed types within each season.
The statistical package JMP (SAS Institute 1989) was used for
all these analyses.

Part II: Infestation Rate of Seeds by Bruchids: Number of Entry Holes and Seed Mortality

This part of the experiment was established to determine whether differences in oviposition rates on different fruit types translated to differences in larval infestation rates. Because mortality can occur at several stages, both the entry and development stages were monitored:

Entry stage. If beetles prefer to lay eggs on certain fruits because they have a better chance of surviving the egg stage and penetrating the endocarp, then the fruits that have more eggs should show a higher ratio of entry holes:eggs laid than non-preferred fruits.

Development stage. Both increased number of eggs and increased endocarp penetration should lead to an increased chance of seed infestation. The fruits preferred by bruchid beetles should also be the ones most likely to be destroyed by larvae.

The endocarps from Part I were left in their exclosures in the field for approximately three months. This was the time period that both lab experiments and field observations indicated was sufficient for most larvae to reach full size and consume all the endosperm, but not sufficient to allow pupation and emergence. The three month period was counted from the day each experiment was set up, so that different

set ups were collected on different days and in different months. The length of time endocarps remained in the field averaged 99 days in June (range 92-102 days), 103 days in July (99-106 days), and 86 days in September (78-93 days).

After collection, all seeds were measured along the long axis, and the number of visible entry holes counted (regardless of whether they penetrated to the endosperm or not). Each endocarp was then split open with a machete, and the following parameters assessed: number of seeds, amount (estimated proportion) and condition (germinating, with fungus, or intact) of seeds not eaten by larvae, number and developmental stage of bruchids, if any (larva, late larva, pupa, or adult), and identity of parasites on bruchids, if any.

Data Analysis, Part II

The number of entry holes and the proportion of infested seeds for each category were compared within each season with a Kruskal-Wallis test. Unlike the situation in Part I, endocarps derived from Intact Husk fruits were included in the analysis in Part II.

The stage (small larvae, large larvae, late larvae, pupa, and adult) of all larvae obtained were compared among seasons with a Chi-Square test for all fruit types grouped (due to the large number of blank cells). For the September data set only, the larval stage was compared among fruit

types with a Chi-square test, because all larval stages were well represented. The statistical package Statview (Abacus Concepts 1986) was used for these analyses.

Control Experiment

To determine whether seven nights of exposure to oviposition are sufficient to lead to high levels of seed infestation under the controlled conditions of the experiment, a small scale experiment was set up among the experimental trees. Fifty Gashed fruits were protected by a chicken wire exclosure and exposed to oviposition for seven nights, then covered with mosquito meshing to exclude bruchid beetles and left in the forest. Another 50 fruits were placed next to the above exclosure, protected only with chicken wire. After three months the endocarps were collected, the number of entry holes counted, and the endosperm and larvae described as in Part II above. A t-test was used to compare the number of entry holes on the two sets of seeds, and the proportion on infested seeds was compared visually.

Results

Intact Husk fruits received no eggs during the first and second checks, with the exception of two fruits that were bitten open by insects and mammals, respectively (Table 3-1).

Only by the sixth week in the field had at least one Intact Husk fruit in all set ups received eggs. This occurred when the husk had rotted sufficiently to split, or to lift away from the pulp, opening a gap at the seed's proximal end between husk and endocarp. Eggs were laid both on the husk and the pulp at this stage. The number of eggs remained low, with no fruit ever receiving more than 8 eggs, and the mean number of eggs per fruit ranging from 0.3 to 1.15 for different set ups (Table 3-2).

The number of eggs found on Gashed, Rodent, Intact Pulp, and Bare Seed fruit types after 7 nights (mean 6.86 eggs/fruit, range 0-47) was greater than the number of eggs after one night (mean 3.36 eggs/fruit, range 0-26), but the relative differences among seed types remained the same on both checks. Only the results of the second check are further described. The total number of eggs and the variation among fruits in number of eggs decreased markedly during the study, both among and within seasons, for the other fruit types (Fig. 3-2a-d, Fig. 3-3). The decrease was much more marked for Gashed and Rodent fruits than for Intact Pulp and Bare Seed fruits (Fig. 3-2a-d). I describe first the trends, and later the significant differences among fruit types.

In June, Gashed and Rodent fruits set at the end of the month had fewer eggs than those set earlier in the month (Fig. 3-2a-b), but the same was not true for Bare Seed and Intact Pulp fruits (Fig. 3-2c-d). Gashed and Rodent fruits received the highest number of eggs in all seasons, but in

June Rodent fruits had more eggs than Gashed fruits (18.9 vs. 15.9 eggs per fruit), a difference that was reversed in July and September. Intact Pulp fruits consistently received the lowest number of eggs in all seasons (4.6, 2.5, and 2.1 mean eggs per fruit respectively), followed by Bare Seeds (6.6, 3.0, and 2.7 eggs). For the five trees that were checked after 14 nights, Intact Pulp fruits averaged 8.0 eggs/fruit and very few of the original eggs had hatched, indicating that they were still receiving eggs and that the first eggs laid were not successful.

These differences were consistent among trees within each season (Fig. 3-4a-c). In June, a marked difference among trees in total number of eggs received, and a reduction in the difference between Gashed and Rodent fruits were due to the spread in time of experimental set ups, with the trees used later in the season having both fewer eggs and a similar number of eggs on Gashed and Rodent fruits (Fig. 3-4a).

A 2-factor ANOVA on log transformed data revealed significant effects of both Fruit Type (df = 3, F = 39.94, p < 0.0001) and Season (df = 2, F = 43.74, p < 0.0001), and a significant interaction between Season and Fruit Type (df = 6, F = 2.26, p = 0.0437). Post hoc comparisons indicated that in all seasons, Gashed and Rodent fruits are statistically indistinguishable from each other, as are Bare Seed and Intact Pulp fruits. In June and July, Gashed and Rodent fruits receive significantly more eggs than both Bare Seed and Intact Pulp fruits. In September, the significant

difference between Rodent fruits and both Bare Seeds and Intact Pulp disappears, but Gashed retains significantly higher numbers of eggs than Bare Seed and Intact Pulp.

When the seasons are compared to each other, without regard to fruit type, in June significantly more eggs were laid than in both July and September, but the latter two are statistically indistinguishable from each other.

Control Experiment

After three months, there was no significant difference in the number of entry holes on endocarps exposed to beetles for 7 nights (15.3 +/- 6.31 holes) and those exposed for the full three months (16.1 +/- 5.72 entry holes; t = 0.42, p = 0.338). Both endocarp types had the same larva-induced mortality rate (Table 3-3). The only apparent difference between the two sets of endocarps was that nine of the larvae in the three month exposure set had been parasitized/killed by insects, whereas there was no indication of parasitism in the seven night exposure set.

Phase II: Entry Holes

The number of entry holes was significantly different among fruit types in all seasons (Kruskal Wallis, H = 280.78, 135.64, and 75.33 respectively in June, July, and September,

p = 0.0001 in all cases). The trends in entry holes followed those expected from the number of eggs for all seed types in all seasons, with the exception of Intact Pulp fruits. Although this fruit type always had the lowest number of eggs, behind Bare Seeds, in June it had the second lowest number of entry holes, ahead of Bare Seeds, and in July and September it had the same number of entry holes as Rodent, and more than Bare Seeds (data are mean of all seeds per fruit type). This discrepancy suggests that once the pulp became degraded some time after the second check, beetles continued laying on Intact Pulp fruits, and this latter round of egg-laying produced larvae that successfully entered the seed. Therefore, as for Intact Husks, the number of eggs counted at the second check does not correspond to the actual egg laying intensity eventually experienced by the seeds.

For the three other fruit types, the second check egg count should be a good index of the larval cohort that will attempt the first entry to the seed. Excluding the Intact Husk and Intact Pulp fruits for the reasons explained above, the ratios of entry hole number:egg number in June, July and September for each seed type are as follows: 0.539, 0.367, and 0.390 for Bare Seed; 0.826, 0.754, and 0.610 for Gashed, and 0.788, 0.692, and 0.504 for Rodent. These larval success ratios reflect the laying preferences of beetles; fruit types with the highest success ratios in each season received the highest number of eggs. Additionally, the seasonal decrease

in egg:entry hole ratio indicates increasing egg mortality
from June to September.

Part II: Proportion of Endocarps Infested by Larva

An endocarp was considered infested if it contained: any
live or dead larval stage or adult beetle, the parasites of
bruchid beetles, the track of a larva through the endosperm,
or larva frass. Any endocarp that had at least one larva was
classified as infested, even if, in the case of multiple
seeded endocarps, one of the seeds was still intact.
Although in a natural (unprotected by exclosures) setting one
seed of multiple-seeded endocarps sometimes escapes predation
(Fragoso 1994), in this experiment very few endocarps showed
this situation (9 Intact Husk fruits, 3 Intact Pulp fruits, 2
Gashed fruits, 2 Bare Seed fruits, and 1 Rodent fruit).
Large larvae used all seeds within an endocarp, and when one
seed was still intact, the larvae was usually small and still
had the chance of destroying all seeds. The difference
between the experimental and the natural settings is that the
wire cages protected seeds (and eggs) from trampling,
shifting, and pulp removal, therefore giving the eggs and
first instar larva a much better chance of hatching and
entering, respectively.

All fruit types in all seasons had a nearly 100%
infestation rate with the exception of Intact Husk (mean
infestation rate 60% +/- 32) in June. Thirty seven Intact

Husk and 9 Bare Seed endocarps survived in June, compared to only 1, 1, and 0 Intact Pulp, Gashed, and Rodent endocarps respectively (Table 3-4). The difference in survival rate among seed types was significant in June (Kruskal-Wallis test, H = 16.08, p = 0.0001; based on mean survival rate per seed type per tree), but not significant in July and September (p = 0.07 and 0.4, respectively). Note that the sample sizes for Intact Husk and Intact Pulp fruits were reduced in July and September compared to other fruit types due to fruit removal by vertebrates.

The seed survival rate for IH fruits was significantly higher in June than in July and September, and was not different between July and September (X^2 = 67.3, p = 0.0001, DF = 8) (Table 3-5).

Bruchid Stage

In June and July, most of the larvae found in all fruit types were large, late instar larvae that had consumed all or most of the endosperm in their seeds (Table 3-6). Two exceptions were Intact Husk fruits in June and July, which had a high proportion of very small larvae, indicating that larvae were younger than those in the other fruit types, as would be expected from the late timing of egg-laying on these fruits.

In September, 65.5% of larvae found were large larvae, but now a high proportion of seeds contained late larvae,

pupa, and adult beetles (30% combined late stages) (Table 3-5). Within this season, Bare Seeds had a disproportionately high number of late stages (53.7% combined). The combined differences in larval stages were significantly different among seasons (X^2 = 221.47, p = 0.0001, df = 8). Since all seeds were the same age when collected from the forest (in fact, the September seeds were younger by about two weeks than the June and July seeds), these differences indicate that a) larva from eggs laid later in the season developed at a faster rate than those earlier in the season for all fruit types; and b) larvae in Bare Seeds late in the season developed faster than larvae in other seed types in the same season. This early development in Bare Seed fruits was already noticeable in July, when a higher percentage of larvae in Bare Seeds than in any other fruit type were late instar larvae (Table 3-6)

Fruit and Seed Loss to Vertebrates and Invertebrates

Fruit disappearance from exclosures were greater late in the fruiting season than earlier (Table 3-7). In June, fruit disappeareance occurred without exclosures being breached. In July and September, some but not all exclosures with fruit loss were breached, and in some cases chewed fruits were found within the uplifted exclosure.

In one exclosure where four Intact Pulp fruits were lost in September, without exclosure disturbance, only three

endocarps were found on the surface in December. Persistent digging uncovered all seven missing endocarps, individually buried about 10 cm under the soil surface, within the area protected by the exclosure. Of these seven endocarps, four were intact, two had very small larvae with 80 % of the endosperm intact, and one had a large larvae that had consumed all the endosperm. The other 40 endocarps set at this tree were all infested or their seeds had rotted. At the time that the first four fruits were buried, at least two of them had received at least 1 or 2 eggs (counted after the first check). At the second check, the six remaining Intact Pulp fruits had 0, 1, 1, 2, 3 and 4 eggs respectively, so that when the final three were buried, an unknown time after the second check, at least two of them had at least one egg on them. In other words, a maximum of three fruits could have been buried with eggs already on them.

Discussion

Implications for Fruit Handling by Animals

The most striking differences in both ovipostion and seed survival rates occurred between Intact Husk fruits and all other fruit types. Female <u>Pachymerus</u> <u>cardo</u> at Maracá did not lay on fruit husks until these began to rot, and even then the number of eggs laid was low compared to the number laid on the other fruit types within the same season. Given

the consumer set that uses _Attalea_ fruits at the Maracá site, the avoidance of intact fruits by bruchid beetles has significant implications for the palm's dispersal ecology and adult distribution pattern.

The seeds that had the best chance of surviving were those that fell to the ground in fruits unhandled by arboreal or terrestrial pulp eaters. These are the fruits that are ingested by tapirs in large amounts and carried long distances from the parent tree (Fragoso 1997b). Because intact fruits do not receive eggs until at least four weeks after falling, they are uninfested at the time of ingestion by tapirs. After defecation, they are subject to infestation by bruchids in the feces (Silvius pers. obs.), but the infestation rate in the feces is much lower than in the original fruit piles (Fragoso 1997b).

The fruits with the highest probability of receiving eggs are those that have been handled by the presumed best dispersers (rodents, primates and spit-dispersing ungulates) and also by procyonids and psittacines. Although the increase in egg laying did not result in an increase in larval infestation in the experiment once Intact Husk fruits are excluded, it must be remembered that the fruits in the experiment were protected to an extent that would not occur naturally. Foraging tapirs, peccaries and deer trample seeds into the ground, and falling litter protects them from access by beetles (as does burial under the fruit pile). Therefore the longer a fruit remains without eggs, the more likely it

is to survive infestation. Rodent and Gashed fruits always received eggs after the first night. However, since eggs do not hatch for several days, it is unclear how well oviposition translates to first instar survival if seeds are subsequently trampled or buried. Eggs laid on Rodent and Gashed fruits are more likely to remain attached to the seed than those laid on intact pulp, however, and therefore more likely to resist partial burial.

These observations refer to endocarps remaining unburied near the parent tree. Squirrels probably bury many endocarps throughout the fruiting season, and agoutis bury some seeds late in the season (Fragoso 1997b). Fruits dispersed by primates even within several hundred meters of a tree are still exposed to high rates of oviposition, at least within a forest with high Attalea density (fruits placed up to 200 meters from the nearest fruiting palm received the same numbers of eggs as fruits placed at the base of fruiting and non-fruiting palms; Silvius, unpublished data). Therefore at this time the best chance of survival is to be an Intact Husk or Intact Pulp fruit that gets carried away by a tapir soon after falling. Thus the activities of vertebrate pulp eaters can mediate seed predation by invertebrates when the invertebrate is the primary predator on the seed, as it is in this case, where more than 95% of all seeds remaining on the surface near the parent plant are destroyed by bruchid beetles (Fragoso 1997b, Chapter 4).

Pulp-Oviposition and Pulp-Development Rate Interactions: The
Role of Moisture Levels

The amount of pulp remaining on endocarps, and the
pattern in which it was arranged, had a significant effect on
the number of eggs laid on fruits by bruchid beetles. This
effect translated into higher egg and first instar larva
survival, as indicated by the dependence of number of entry
holes on number of eggs. Fruiting season interacted with the
effect of pulp on both number of eggs and number of entry
holes: overall number of eggs laid, and differences among
fruit types in number of eggs laid, were greater early in the
fruiting season (June) than late (July and September).
Differences in egg laying and egg survival also translated
into differences in seed infestation rates (number of
endocarps with at least one larva entering), but this effect
was significant only in June, when larva failed to penetrate
Intact Husk fruits.

The general trend in egg laying preference was that
endocarps with some pulp were preferred above endocarps with
no pulp or with too much pulp. Fruits with intact husks were
inaccessible to ovipositing females. Avoidance of seeds with
large amounts of pulp may be due to at least two factors: a)
first instar larvae are unable to penetrate the pulp for
either physical or chemical reasons, and b) eggs do not stay
attached very well to intact, slimy pulp. Both possibilities
are supported by the observation that female bruchids often

lay eggs on pieces of litter stuck onto Intact Pulp fruits, on indentations in the pulp made by pulp eating invertebrates, or at the proximal end of the seed, where the pulp layer is thinnest. The second possibility is supported by the fact that eggs on intact pulp frequently fell off when handled or after heavy rainfall.

On Bare Seed fruits, females usually laid eggs on the underside of the endocarp. Wright (1991) observed the same behavior for a different palm bruchid species in Panama. Along with the above observations on pulp condition, this behavior suggests that moisture is a key factor in egg-laying choice: eggs on bare endocarps are likely to dry out, because there is no pulp to retain moisture. Eggs on intact pulp will not dry out, but neither do they stick well. Fruits gnawed by rodents and gashed by ungulates or monkeys, on the other had, provide a secure attachment site on the bare endocarp or on the juice-free fiber, while providing moisture-retaining pulp or fiber. On Gashed Fruits, eggs were nearly always laid on the endocarp but close to or under the edge of the pulp. It is unclear, though, why infestation of completely bare endocarps was lower early in season, when it rained frequently, than later in the season. One explanation may be related to the observed higher insect-related egg mortality on bare endocarps than on fruits with pulp.

The net effect of these seasonal differences was that even though oviposition rates were higher early than late in the fruiting season, seed survival was also higher early than

later. In other words, the correlation between oviposition rates and survival is strong within a season but does not carry on across seasons. Early in the season, Intact Husk and Intact Pulp fruits resisted beetle infestation long enough that, had they not been protected by exclosures, they had better chances of being removed by a disperser before bruchid eggs could hatch or even be laid on them. Therefore trees fruiting late in the season, when bruchid activity is lower, do not necessarily have higher seed survival probabilities, as predicted by Forget et al. (1994) and Wright (1990) for a similar system in Panama. Those authors' conclusions were based on monitoring of egg numbers only, and not on the translation from egg to larval infestation rates. On the other hand, late in the season, when overall fruit pulp availability is lower in the forest (Chapter 6), fruit removal rates by frugivores may be higher, as indicated by the invasion of exclosures in the last experimental set up. In this case seed survival would depend on whether frugivores remove seeds to a site that protects them from bruchids. On Maracá, bruchid activity is so high (compared to the mean 1-2 eggs per endocarp documented during the peak fruiting season on BCI, Wright 1990) that fruits placed more than 100 meters from fruiting trees have the same likelihood of being found by bruchids as fruits near the tree (Silvius, unpublished data).

The role of moisture seems to be important in another way. Several researchers have observed that rainfall may cue

the emergence of adult beetles(Janzen 1971, Wright 1983).
The more rapid development of larvae late in the season on
Maracá (endocarps from the September replicate were collected
in December, two months into the dry season, whereas those
from June and July were collected in September and October,
respectively), and the more rapid development of larvae in
Bare Seeds (the ones most likely to lose moisture) suggest
that beetles may be responding to the moisture level in the
environment by speeding development when moisture is low.
Thus, most beetles emerge in the dry season, regardless of
when the eggs that gave rise to them were laid. With a few
exceptions, emergence from natural, non-manipulated endocarps
in the field did not begin until November, and did not reach
its peak until December-January (Chapter 4), supporting these
observations. An alternative hypothesis is that there are at
least two sub-populations of beetles, that differ genetically
or behaviorally with respect to reproductive traits: one
group that lays early in the season but emerges late, and
another that lays late in the season but emerges early.

Pulp as Protection

The interaction between pulp eaters, bruchid beetles,
and palm fruits also indicates that pulp, as well as husk,
can be a protective mechanism against invertebrate seed
predators. It may be under selective pressure for this
reason as well as for its attractiveness to dispersers. The

role of husks (pericarp or exocarp) as physical deterrents against invertebrates has received some mention in the literature (e.g., Pritchard 1969, Sallabanks and Courtney 1992, Rodgerson 1998), and the role of chemical deterrents in pulp has been extensively investigated (see reviews in Herrera 1982, Sallabanks and Courtney 1992, and Cipollini and Levey 1997), but I have found no mention of pulp as a physical deterrent.

Work by Delgado et al. (1997) suggests a similar role for pulp in a different palm species. These authors found that oviposition by bruchid beetles on Astrocaryum chambira fruits, which have a much drier, thinner mesocarp than Attalea fruits, was more rapid on peeled than intact fruits, and that oviposition became high on unpeeled fruits only after the mesocarp had decayed. Because Astrocaryum seeds are prized by many granivorous rodents (Smythe 1986, Terborgh et al. 1993, Cintra and Horna 1997, Hoch and Adler 1997), if pulp protects a fruit on the ground until rodents scatterhoard them, then the fruit's chance of survival is increased. This type protection would also work with the putative megafauna dispersers that may have coevolved with large-fruited tropical trees (Janzen and Martin 1982), represented today only by the tapir (Fragoso 1997b).

Burial by Scarabid Beetles

The seven fruits "lost" from the September exclosure were buried at a depth and in a pattern typical of burial for nesting purposes by large scarabid beetles of the burrower type (Halffter and Edmonds 1982). Several observations indicate that the seven fruits were buried by the dung beetle Oxysternon festivum (Scarabaeidae / Coprinae / Phanaeini) and that burial of Attalea fruits by this species is a common occurrence at this study site. Adult scarabid beetles have been recorded feeding on pulp (Hanski and Camberfort 1991), and one species is known to synthesize nesting balls out of pulp and other plant parts (Monteith and Storey 1981), but I know of no reports of scarabid beetles using entire fruits to provision their nests. During a study scarabid beetles on Maracá in June 1996, large numbers of the beetles were captured in traps baited with fox (Cerdocyon thous) dung (which at that time contained Guava pulp and seeds), and was considered a common species in the study area (F. Vaz de Mello, pers. comm).

On two occasions the beetles were observed to bury Intact Pulp Attalea fruits shallowly in a network of tunnels under fruit piles, in a manner similar to that of shallow burial of dung balls for adult feeding by other dung beetle species. A beetle captured at a fruit pile and held in the lab for a few hours buried five Intact Pulp fruits to a depth of 5 cm, the maximun depth of soil provided in its container.

Throughout the five fruit type experiment described in this paper, fruits were found within the exclosures shallowly buried in the beetle fashion. Only the fruits from the single tree in September, described above, were ever found deeply buried. Thus, <u>Oxysternon</u> exhibited the two kinds of food burial typical of dung beetles: shallowly buried fruits on which adult beetles may feed, and deeply buried fruits potentially used as food for larvae.

The seven exclosure fruits deeply buried by the beetles had variable numbers of eggs on them when buried. It would appear that those that were buried early had their eggs scraped off or killed by the burial process. The others survived burial and bruchid larvae infested the seeds, but burial seems to have delayed the development of the larvae in at least two seeds. The higher survival rate of scarabid-buried seeds than of other seeds set at the same tree suggests that burial by scarabids functions in the same way as removal of intact fruits by tapirs: they decrease the chance of oviposition and/or first instar survival. The germination biology of <u>Attalea</u> is unstudied, and it is therefore unclear whether its seeds are able to germinate from a 10 cm depth is unknown. Survival is likely, however, given that many palms have remote germination in which seedlings usually grow down into the soil before extending up to break the surface (Tomlinson 1990). Scarabid beetles could thus be an effective "planter," if not mover, of palm seeds, and many of the seedlings that germinate near the

parent plant on Maracá (Fragoso 1997b) may be the result of burial by beetles rather than by rodents.

Large scale effects of pulp-vertebrate-beetle interactions

This study documented a small-scale interaction at the individual seed level. It further focused on a single forest type with a characteristic mammal community. The distribution of frugivores at a larger scale, however, is patchy and non-random, both on Maracá and at other Neotropical sites. On Maracá, spider monkeys do not use forests near the river (Nuñes 1992), while squirrel monkeys prefer those forests as well as other edge habitats (Silvius pers. obs.). Tapirs prefer to feed in the highest density Attalea patches in the river forest, leading to high levels of intact fruit removal there. At a scale much larger than that of this study, patchiness in frugivore distribution could therefore result in patchiness in palm-beetle-vertebrate interactions and in palm seed survival and regeneration. Such patchiness in interactions could contribute to the clumped distribution of many palm species, a distribution that has most often been attributed to anthropogenic effects (Balée 1988, Clark et al. 1995) or edaphic factors (Kahn and de Granville 1992).

Table 3-1: Timing of egg laying on Intact Husk fruits,
presented as number of experimental setups (trees) out of the
total set up that had at least one egg on at least one fruit
at the time of checking. Data is cumulative. Check # 1
occurred one day after seeds are laid out, subsequent checks
followed at 7-day intervals. A blank cell indicates fruits
were not checked at that date. Egg laying does not begin
until the husks begin to rot and the pulp or endocarp is
exposed.

Check   Number

Season	1	2	3	4	5	6	7	8	9
June 10 trees	0	0	4	6	7	9	10	10	10
July 10 trees	0	1*	4**	6	6	9			
September 8 trees	0	1**							

* = husk chewed open by insects, exposing the pulp.
** = husk chewed open by mammals, exposing the pulp

Table 3-2: Mean number and range of eggs per fruit for trees
that received eggs on the Intact Husk fruits during the June
experiment, by check. n = 100 seeds per check (10 seeds at
each of 10 trees).

Mean	0	0	0.3	0.28	0.87	0.83	1.15	0.9	0.92
Range	0	0	0-1	0-2	0-5	0-4	0-8	0-5	0-6

Table 3-3: Infestation rates for fruits exposed to bruchid
oviposition for seven nights and three months, respectively.

	7 night exposure	3 month exposure
Large Larvae	45	46
Empty Endocarp	3	4
Rotten Endosperm	2	0
Total	50	50

Table 3-4: Seed survival per fruit type and season, presented as number of infested (at least one endosperm with larvae or other sign of bruchid beetle infestation), good (no seeds with larvae or sign of infestation) and other (empty endocarp or endosperm rotted by fungus, with no sign of bruchid infestation). Note reduction in sample size for IH fruits in all seasons and for IP fruits in July and September, due to fruit loss from the exclosures to pulp consumers.

June (initial n = 100 fruits per fruit type.

	Infested ($\geq$ 1 seed infested)	Good (no seeds infested)	Other (empty, fungus)
Intact Husk	57	36	2
Intact Pulp	98	1	1
Bare Seed	86	9	5
Gashed	96	0	4
Rodent	95	1	4

July (initial n = 100 fruits per fruit type)

	Infested ($\geq$ 1 seed infested)	Good (no seeds infested)	Other (empty, fungus)
Intact Husk	91	3	0
Intact Pulp	90	3	4
Bare Seed	97	0	2
Gashed	99	0	1
Rodent	92	5	5

September (initial n = 80 fruits per fruit type)

	Infested ($\geq$ 1 seed infested)	Good (no seeds infested)	Other (empty, fungus)
Intact Husk	58	0	4
Intact Pulp	68	4	1
Bare Seed	78	0	1
Gashed	76	0	2
Rodent	78	0	1

Table 3-5: Seed survival in Intact Husk fruits during the three seasons. Survival is significantly higher in June than in July and September ($X^2 = 67.3$, p = 0.0001, df = 8)

Season	Infested	Good	Other
June	57	36	2
July	91	3	0
September	58	0	4

Table 3-6: Infestation stage of endocarps, separated by fruit type and season. "New larvae" are small larvae that have not had time to eat much of the endosperm; "larvae" are large larvae that have eaten all or most of the endosperm but have not metamorphosed into pupal stages, "late larvae" are larvae that have started to metamorphose, as indicated by a reduction in size, thickening of body and change in head shape; "pupa" are soft, white with legs, mouth parts and wings; adults are dark, fully formed beetles. Field age is the number of days the seeds remained in the forest between setting and cracking; for all endocarp types except Intact Husk, this corresponds to larval age.

June (mean field age = 99 days)

	New Larvae	Larvae	Late Larvae	Pupa	Adults	Total
Bare Seed	4 (5%)	75 (94%)	0	1 (1%)	0	80
Intact Husk	14 (26%)	39 (74%)	0	0	0	53*
Intact Pulp	3 (3%)	89 (97%)	0	0	0	92
Gashed	1 (1%)	87 (99%)	0	0	0	88
Rodent	1 (1%)	86 (98%)	1 (1%)	0	0	88
Total Larvae	23 (5.7%)	376 (93.7%)	1 (0.25%)	1 (0.25%)	0	401

* Low number of larvae in IH seeds is due to low infestation rate of seeds during the first part of the experiment.

Table 3-6, continued:

July (mean field age = 103 days)

	New Larvae	Larvae	Late Larvae	Pupa	Adults	Total
Bare Seed	5 (5%)	80 (83%)	10 (10%)	2 (2%)	0	97
Intact Husk	23 (25%)	65 (72%)	2 (2%)	1 (1%)	0	91
Intact Pulp	4 (4%)	86 (96%)	0	0	0	90
Gashed	2 (2%)	91 (98%)	0	0	0	93
Rodent	1 (1%)	86 (99%)	0	0	0	87
Total Larvae	35 (7%)	408 (89%)	12 (3%)	3 (1%)	0	458

September (mean field age = 86 days)

	New Larvae	Larvae	Late Larvae	Pupa	Adults	Total
Bare Seed	2 (2%)	40 (44.4%)	22 (24.4%)	23 (26%)	3 (3.3%)	90
Intact Husk	8 (13%)	29 (48%)	16 (27%)	7 (12%)	0	60*
Intact Pulp	4 (6%)	55 (76%)	7 (10%)	5 (7%)	1 (1%)	72
Gashed	1 (1%)	66 (79%)	8 (9.5%)	9 (10.5%)	0	84
Rodent	2 (3%)	55 (82%)	6 (9%)	4 (6%)	0	67
Total Larvae	17 (4.5%)	245 (65.5%)	59 (16%)	48 (13%)	4 (1%)	373

* Low number of larvae in Intact Husk seeds is due to loss of seeds to frugivores during experiment.

Table 3-7: Fruit losses from exclosures after one week.

Season	Fruit Type	Number Lost
June	Intact Husk	5
July	Intact Husk	6
	Intact Pulp	2
	Bare Seed	1
September	Intact Husk	18
	Gashed	2
	Rodent	1
	Bare Seed	1
	Intact Pulp	4

One Tree = One "Experimental Set-Up" = One Replicate

X 10 = One Season or Experiment
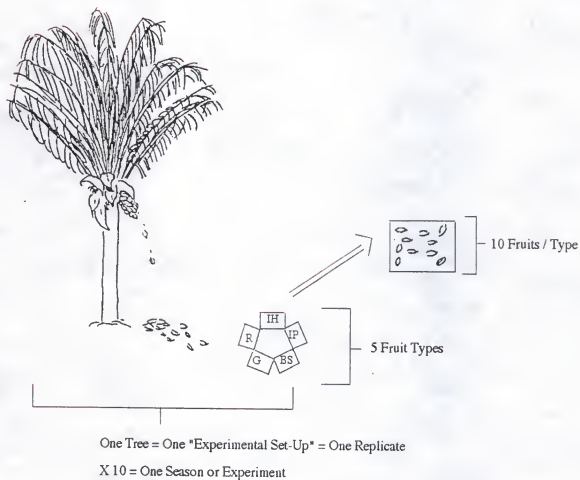
Figure 3-1. Experimental field design for Parts I and II.
IH = Intact Husk fruits, IP = Intact Pulp fruits, BS = Bare
Seed fruits, G = Gashed fruits, R = Rodent fruits. See text
for fruit type descriptions.
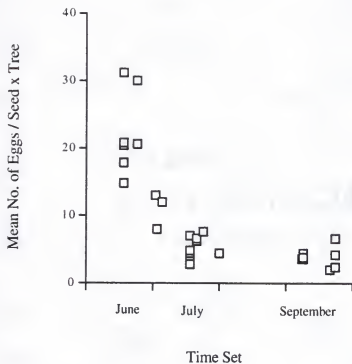
a) Rodent

Figure 3-2. Mean number of eggs laid by bruchid beetles on sets of 10 fruits of 4 different fruit types at each of 10, 10, and 8 trees in June, July, and September, respectively. a) Rodent gnawed fruits; b) Primate or ungulate gashed fruits; c) Endocarps with all pulp removed; d) Fruits with pulp intact but all husk removed.
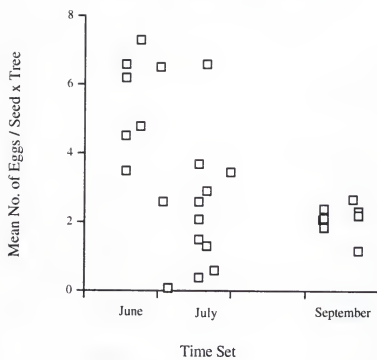
Time Set
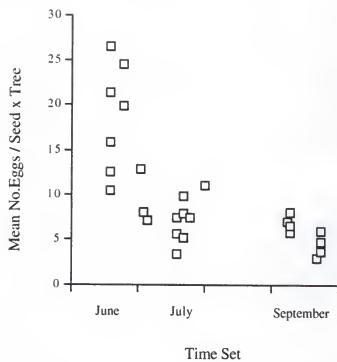
b) Gashed

Figure 3-2, continued.
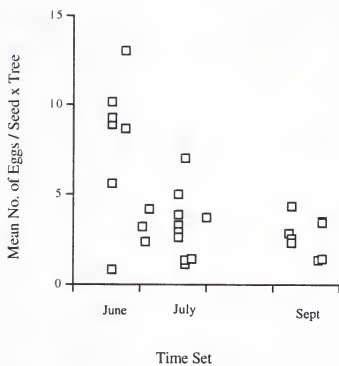
c) Bare Seeds

Figure 3-2, continued.
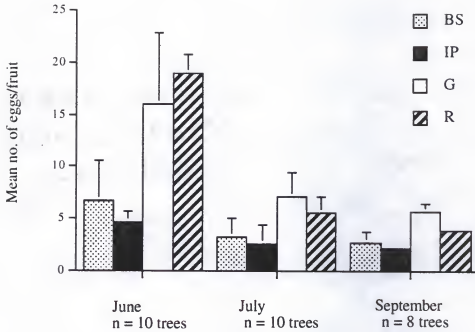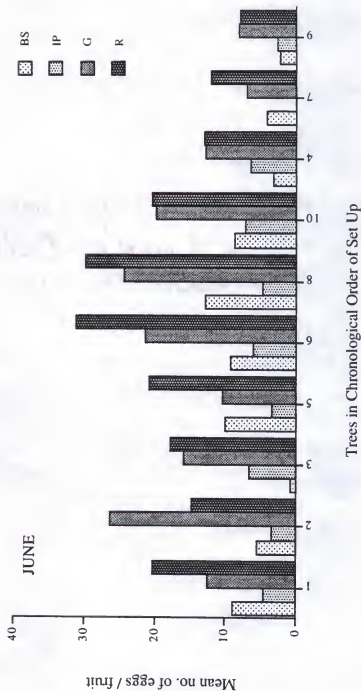
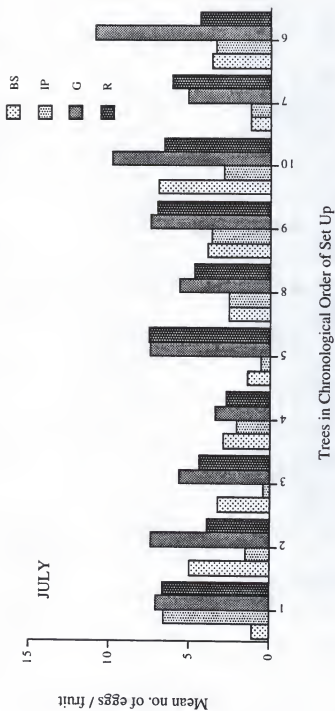d) Intact Pulp

Figure 3-2, continued.

Figure 3-3. Mean number of eggs on all fruits at all trees for each fruit type, with standard error, showing the high oviposition intensity in June, and the low oviposition intensity in July and September. IH = Intact Husk fruits, IP = Intact Pulp fruits, BS = Bare Seed fruits, G = Gashed fruits, R = Rodent fruits.

a)

Figure 3-4. Mean number of eggs on all fruits of each fruit type at each tree, showing that differences in oviposition rates among fruit types were similar across trees. a) June, b) July, and c) September. IH = Intact Husk fruits, IP = Intact Pulp fruits, BS = Bare Seed fruits, G = Gashed fruits, R = Rodent fruits. See text for fruit type descriptions.

b)

Figure 3-4, continued.

SEPTEMBER

Mean no. of eggs / fruit

Trees in Chronological Order of Set Up

BS
IP
G
R
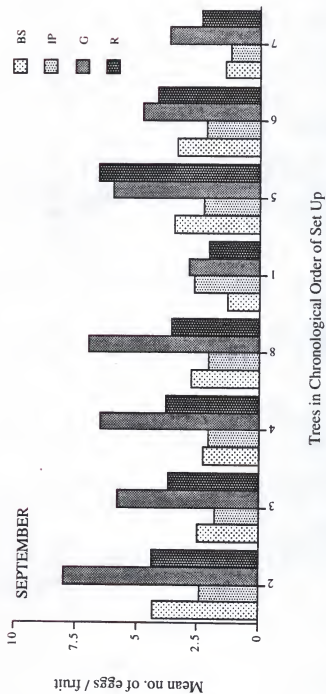
c)

Figure 3-4, continued

PALM ENDOCARP USE BY THREE NEOTROPICAL SEED-EATERS: GRANIVORY
OR "GRUBIVORY?"

Introduction

Palm fruits are an important component of Neotropical
mammal diets. Primates feed on mature palm pulp and immature
endosperm, and in some cases on old "nuts" (endocarp plus
contents) remaining on the ground for up to a year after the
fruiting season (Chapter 2). Terrestrial mammals, including
ungulates, rodents, marsupials, and carnivores, use the pulp
and crack or gnaw open fresh and old nuts (Chapter 2).
Because they are protected by thick endocarps, palm seeds may
remain available on the ground for longer periods of time
than softer fruits or seeds.

By virtue of their thick endocarps, coccosoid palms in
particular provide ideal sites for the growth and
metamorphosis of palm bruchid beetles (Coleoptera: Bruchidae:
Phachymerini). Palm-bruchid interactions are especially
well-developed between _Attalea_ sp. and _Astrocaryum_ sp. palms
and _Pachymerus_ sp., _Caryoborus_ sp., and _Speciomerus_ sp.
beetles (Delobel et a. 1995, Johnson et al. 1995, and Johnson
1993). The beetles' large, lipid-rich larvae feed on the
endosperm and remain inside the endocarp for three to nine

months (Chapter 2, 3). Beetle infestation rates can be very high for seeds remaining near the parent tree or within an aggregation of palms. For non-manipulated seed piles, Janzen 1971 and Fragoso 1997b documented 80% and 77% respectively of seeds killed by bruchids; for experimentally cleaned seeds, Smythe 1989 and Terborgh et al. 1993 documented 98% and 75% mortality, respectively.

When vertebrates feed on endocarp contents, they are therefore likely to interact with bruchid beetles as well as with palm seeds. Not only do they kill bruchids and potentially affect the population dynamics of both the beetle and the palm (as suggested by Forget et al. 1994 for palm bruchids, and Herrera 1989, Traveset 1992 for other beetle species), they also enter into an evolutionary relationship with the palm-beetle complex (c.f. Herrera 1984).

There is evidence that in several frugivory systems, both pulp and seed eating vertebrates actively seek out invertebrate pests on fruits and seeds. Redford et al. (1984) experimentally showed that marmosets prefer fruit pulp infested by insect larvae. Through field and cage experiments, Vaulberg (1992a,b) showed that at least one species of understory bird preferred infested to non-infested pulp. Scott and Black (1981) demonstrated that cockatoos feeding on weevil-infested <u>Banksia</u> infructescences were searching for larvae. In other cases, consumers ingest fruits irrespective of the infestation state (Herrera 1989,

Piper 1986); i.e., they do not reject them because they contain insect larvae.

In the case of thick-endocarp palms, several authors have suggested that vertebrates incidentally feed on larvae (Janzen 1971, Kiltie 1981). Others have suggested that they actively seek out bruchid larvae (Robinson 1986, Struhsaker and Leland 1977). Fragoso (1994) showed that white-lipped peccaries (_Tayassu_ _pecari_) in captivity will crack infested endocarps and ingest the larvae. Terborgh (1983) describes _Cebus_ _apella_ preferentially opening endocarps that have been infested, because they are easier to open, but suggests that the primates are seeking endosperm remains rather than larvae.

If vertebrate consumers feed on larvae from insect-infested fruits and seeds, then measures of food availability for fruit and seed eaters must take into account the availability and development patterns of these insects. In particular, estimates of seasonal food scarcity (c.f. Terborgh 1986a,b, Leigh et al. 1996) that rely on counts of mature fruits may not accurately reflect true availability in the environment. For one rain forest site in the northern Amazon, this study asks whether vertebrates seek out bruchid larvae in palm endocarps, and whether they do so at the time of low fruit availability. I examine the timing of availability of _Attalea_ _maripa_ endocarp contents--either endosperm or larvae--with respect to the availability of other fruits and seeds in the habitat. I monitor the timing

of endocarp use by squirrels (*Sciurus igniventris*), agoutis (*Dasyprocta agouti*), and white-lipped peccaries, three species that differ both in their degree of dependence on seeds and in their ability to access a habitat mosaic that can provide a wide range of foods during the season of fruit scarcity.

Study Site

Maracá Island Ecological Reserve, a 1,100 km^2 riverine island in the northern Brazilian state of Roraima, lies on the forest side of the forest-savanna boundary between the Rupununi savannas of Guyana and the Amazonian rain forest. Habitats grade from small savannas, transitional forests, and high diversity moist upland forest on the eastern end of the reserve, through an area dominated by the deciduous legume *Peltogyne gracilipes* in the center and center east, and moist upland mixed forests on the western half. The eastern terrain, where this work was carried out, is flat and low (110-160 meters above sea level). The sandy soils are derived from quartz-biotite schists, quartz-feldspar gneisses, and tonalitic granites (Thompson et al. 1992).

Rainfall records on the eastern end of the island show variation between 1,750 and 2,300 mm annually; during El Niño years, rainfall decreases markedly across the state. The wet season is between May and September, the dry season between October and April, with rains starting either in early or late

April. The heaviest individual rains tend to fall in the dry season.

There are no extensive flooded forested habitats or palm swamps in the Reserve, although the riverine forest floods in low pockets during high rainfall years (Fragoso 1994). Several small ponds and savannas are interspersed throughout the forest, and frequent strands of _Mauritia_ palms run along stream courses and other periodically flooded habitats. The plant families with the greatest number of tree species on terra firme habitats are the Leguminosae, Rubiaceae, Moraceae, and Burseraceae (Milliken and Ratter 1989, 1998). Based on importance value (IV = relative density + relative dominance + relative frequency) rather than species richness, Sapotaceae is the dominant family in the eastern forests. Rubiaceae, Moraceae, Burseraceae, Annonaceae, Chrysobalanaceae, Palmae, and Bignonaceae also occur within the top 5 dominant families based on IV in transects on the eastern end.

Study Species

Individuals of the arborescent palm _Attalea_ _maripa_ (previously _Maximiliana_ _maripa_; taxonomy revised by Henderson 1995) can produce from a few hundred to several thousand 3 to 6 cm long fruits per year (Chapter 3). Endocarp thickness ranges from 1.5 to 6.5 mm. The endocarps of palms in the genus _Attalea_ are thicker and more resistant to rot than those of palms in the genus _Astrocaryum_; to date, reports of

potential bruchid larvae use by non-rodent vertebrates are only for the latter palm genus (Struhsaker and Leland 1977, Kiltie 1981, Terborgh 1983).

White-lipped peccaries are the most omnivorous of the three study mammals, feeding on invertebrates, fish, fruits, seeds, and vegetative plant parts. However, fruits and seeds can make up as much as 60% of their diet (Bodmer 1989). They live in large herds (30-200 animals documented on Maracá), have large home ranges (20 to over 100 km^2, Fragoso 1998), and use a mosaic of habitat types, including terra firme forest, _Mauritia_ palm swamps, savannas, and riverine forest (Fragoso 1994, in review).

The only squirrel species on Maracá, the northern Amazon red squirrel, is a large (500-900 g) animal with terrestrial habits (Emmons and Feer 1997). On Maracá it appears to be common, but is also shy and its ecology has never been studied.

Agoutis on Maracá have an ecology and behavior similar to that described by Smythe (1978) for _Dasyprocta punctata_ in Panama, but have larger home ranges (2.5 to 8 hectares; Chapter 5). Both white-lipped peccaries and agoutis were radio-tracked concurrently with this study.

There are at least three bruchid beetle species on Maracá, but only one, _Pachymerus cardo_, parasitized _Attalea_ palm seeds in this study. Bruchids lay eggs on fallen fruit whose exocarp has been removed by vertebrate consumers (Chapter 3). Within a week, first instar larvae hatch and

tunnel through the endocarp into the seed. Exclosure
experiments and infested seeds kept in the lab indicate that
bruchid beetles require a minimum of two months, and usually
three months, to complete development from egg to adult. The
last larval instar carves a round exit hole almost completely
through the endocarp; after pupation and metamorphosis, the
adult beetle emerges by pushing off the remaining thin "lid"
of endocarp from the hole.

Methods

Overview

Research involved monitoring, in three different
habitats, of forest wide fruit availability, _Attalea_ palm
phenology, and _Attalea_ endocarp use by mammals. Endocarp use
was monitored at three different scales: 1) individual trees
within one habitat, 2) community of trees within one habitat,
and 3) across habitat types. These correspond to the probable
scales of activity of the three seed-eating mammals studied:
individual white-lipped peccary herds move among habitat
types, while individual agoutis and squirrels move among
individual trees in their small home ranges.

The three habitat types studied--riverine forest,
eastern terra firme forest, and central terra firme forest--
differ in their tree species composition and diversity
(Milliken and Ratter 1989). The two terra firme forests have

similar species composition, but palms are more common in the eastern forest, and overall diversity is higher in the central forest. Both have high densities of trees in the Sapotaceae. In contrast, the riverine forest has high densities of <u>Attalea</u> palms, low tree diversity, and almost no trees in the Sapotaceae. Study sites were separated by 5 to 10 km. Monitoring was centered on one 2 km long transect in each habitat, but included additional trails in the eastern forest.

Background Fruit Availability

Fruit availability on the ground was monitored in the three habitats every two to three weeks (range 14-30 days, mean 20.76 days) from November 1995 to October 1996. In the eastern forest, monitoring continued until March 1997. All fruits and seeds seen on the ground along the 2 km by 6 m transects were counted and identified, with each individual item or cluster of items counted as a single patch (fruits separated by more than 10 meters were counted as separate patches if there were no other fruits of the same species in between; if the fruit piles from two adjacent trees overlapped, they were counted as a single patch). Both ripe or newly fallen items and older seeds were counted, and their stage identified (immature, preripe, ripe, rotten, germinating; I define preripe fruits as full sized, immature color fruits). The ground monitoring method was chosen

because agoutis and white-lipped peccaries can only feed on fruit that falls to the ground; because there is a delay in the availability of food items to terrestrial frugivore/granivores compared to arboreal consumers (Zhang and Wang 1995); and because agoutis and white-lipped peccaries feed on older seeds and germinating seeds whose availability would not be measured by canopy observations or fruit trap based sampling. The diet of squirrels on Maracá has not been studied, and the monitoring method may not be an accurate representation of food availability for them. However, dietary studies of a similar species in Central America suggest that this method would have captured many of the important large seeded species, including all palms (Glanz et al. 1996).

Because fruits are rapidly removed by terrestrial animals (Zhang and Wang 1995), a patch-based enumeration was used rather than individual fruit counts, and no attempt was made to estimate the total number or mass of fruits and seeds falling to the ground. Fallen fruit were used as an index of the overall pattern of fruit availability. Although ground transects may fail to capture some fruits that fall to the ground in low numbers (Zhang and Wang 1995), because agoutis feed on large fruits for which remnants of feeding can be found and counted, and because white-lipped foraging leaves obvious signs, this error was minimized.

White-lipped peccaries are able to move between the three habitat types in one or two days. During this study

there were two herds resident in the study area; one herd
included the main trail system in the eastern forest and the
riverine trail in its home range, along with other habitats
on the southeastern portion of the reserve. The second herd
used the main trail system and the area of the central forest
sampled by the transect, in addition to the riverine forest
on the north and north east of the island (Fragoso
unpublished data). Fruit and seed availability at any one
time for white-lipped peccaries is therefore represented by
combining data from all three transects, whereas for agoutis
and squirrels on the main trail system or in the riverine
forest it is represented by just one transect.

Attalea Fruit Availability

In the eastern forest, I located all <u>Attalea</u> trees with
fruits within 20 m of 15 km of trail, starting in April 1996.
On the riverine forest transect, all fruiting trees within 20
m of the 2 km long transect were located and monitored. In
the central terra firme forest, where <u>Attalea</u> is uncommon,
only the few palms (n = 6) that fruited along the 6 m wide
transect were monitored. Trails were checked every two to
three days during the early and peak palm fruiting season
(May-July), to locate as many trees as possible with immature
fruit bunches, and to pinpoint within a few days the start of
fruit fall. After that, trees with near-ripe fruit were
checked at a maximum of one week intervals to ascertain

fruiting data. Based on monitored <u>Attalea</u> trees in all three habitats for which the date of first fruit fall was known or could be estimated, the number of trees starting to fruit during each fifteen day period from April to November 1996 was calculated. The period over which pulp was available was calculated from the median number of days that fruit fall lasted, based on trees for which both the start and end of fruit drop period were noted.

Endocarp Use by Squirrels, Agoutis, and White-lipped Peccaries: Tree- and Within-Habitat Scales

Endocarp use by squirrels and agoutis was studied in the eastern terra firme forest only, while endocarp use by white-lipped peccaries was monitored in all three forest types. In the eastern terra firme forest, endocarps opened by mammals were counted at fruiting trees on a biweekly schedule from April to August 1996, then monthly from August to December 1996, and one final time in February 1997. In December 1996 only a subset of the trees was sampled due to time constraints (20 out of 98 trees available; trees were chosen to be representative of the full spread of endocarp ages available). For the following check (February 1997), the number of endocarps counted at the sub sampled trees was added on to the new data, to match the length of time during which eaten endocarps accumulated for all other trees. Trees were dropped from the census list when treefalls covered the seed pile, when rooting by collared peccaries (<u>Tayassu</u>

tajacu) made it impossible to count seeds, and once the seed pile had been completely depleted by feeding or bruchid beetle emergence.

During each scheduled check I searched an area with a 5 m radius around the tree trunk and counted and removed all endocarps opened by squirrels, agoutis and white-lipped peccaries. Because squirrels ate endocarp contents from perches, if no suitable perches were located within 5 m of the tree, I extended the search radius out to include suitable perches (vines and branches three meters or less above the ground). Both squirrels and agoutis fed on endocarp contents close to the tree, repeatedly using the same feeding site, and endocarp piles were often found in the same location over a period of several months. During a radio tracking study (Chapter 5), agoutis nearly always consumed seeds of all tree species near or under the parent tree, and the same pattern has been found by other researchers (Wenny 1998, Forget 1990, 1993, Smythe 1978). Both squirrels and agoutis fed on endocarps directly from the endocarp pile; squirrels additionally fed on previously buried endocarps, and there was evidence at some trees of digging by squirrels (messier, smaller holes than those dug by agoutis). There was no evidence of scatterhoarding by agoutis near the monitored trees. The number of endocarps located near the parent tree is therefore a good index of endocarp use by squirrels and agoutis; white-lips do not carry endocarps away from the tree.

Each consumer opened the endocarps in a characteristic fashion. On several occasions squirrels were observed feeding on _Attalea_ endocarps, and the opened endocarps were picked up and examined. Squirrel tooth marks were in the form of long gashes, usually in a triangular pattern with a small round hole in the middle. They could be located at either the distal, narrow tip of the endocarp, or at the broad proximal base, by the germination pores. On multiple seeded endocarps, a hole was often made for each seed.

Agoutis were never directly observed feeding on endocarps, but on several occasions I found fresh partially eaten endocarps at sites from which agoutis fled following my approach. The size of the tooth marks was larger than that on the squirrel seeds, and matched the tooth size on the skull of an adult agouti. Holes were in the middle of the endocarp, because agoutis hold onto the ends of the endocarp with their fore feet and gnaw them in a "corncob" fashion. On the side of the seed opposite the hole, the marks of the lower teeth could be seen, where they held the endocarp in place. No other rodents except pacas (_Agouti paca_) and acouchies (_Myoprocta_ sp.) have a gape this wide. Acouchies have not been recorded for the island. Pacas are generally assumed to feed on the pulp rather than the seeds of palms with hard endocarps (c.f. Smythe et al. 1996), but there is no direct information on this, and they are able to scrape away the hard endosperm of _Mauritia_ palms (Prada 1994). Due to the consistency in tooth mark and hole appearance, all

endocarps with centered holes were assumed to have been made by agoutis.

White-lipped peccaries shattered endocarps with a rapid closing of the jaws, leaving splintered woody fragments. Only endocarp tips were counted, to avoid counting multiple fragments of a single endocarp.

Endocarps with tooth marks clearly belonging to small rodents were found inside and at the mouths of hollow logs (too narrow for agoutis), but the consumers were not identified and such endocarps were not searched out.

Counts were not exhaustive, and some endocarps incidentally buried by trampling and other disturbance under shrubs and litter were missed. Endocarp fragments from white-lip feeding were especially difficult to recover; counts of white-lipped cracked endocarps thus always underestimate the actual number opened. Endocarps that could not be aged were not included in the counts. Freshly opened endocarps are lighter and redder in color than older endocarps, and often have endosperm remnants or bits of beetle larvae frass inside. Termites often built nests around and in these hollow endocarps, and this could happen soon after the seed was eaten, masking its age. Because trees were checked frequently, however, new piles were noticed and difficult to age endocarps were few in number.

At the end of the study, all individuals of four tree species known to be important to the three mammals in the study site (_Pouteria surumuensis_, _Pradosia surinamensis_,

Astrocaryum aculeatum, and Attalea maripa) were counted in a
25 m radius area around each monitored tree. The total
number of endocarps eaten per tree, weighted by the number of
days they were available (from the start of fruit fall to the
last check) was calculated and correlated with the abundance
of each tree species using the Spearman Rank Correlation
test.

Endocarp Use by White-lipped peccaries: Across-Habitat Scale

1995 Attalea fruiting season. From November 1995 to
April 1996, endocarp piles remaining from the 1995 Attalea
fruiting season within 6 m of the 2 km long transects in the
three different habitats described above were checked every
two to three weeks during the fruit availability transects
(mean interval 20.76 days, range 14-30 days) for evidence of
use by white-lipped peccaries. Endocarps were not counted or
removed. By April 1996, the few old endocarps that remained
were being covered by new fruits from the 1996 season.

1996 Attalea fruiting season. During biweekly and
later monthly checks from April to November 1996, and again
in February 1997, all seeds opened by white-lipped peccaries
were counted in the riverine and central terra firme forests
as described above for the eastern forest. As was the case
for the eastern forest, in December 1996, only a subset of

the trees available on the river trail was sampled due to
time constraints (18 out of 73 trees available).

Endocarp Contents: Endosperm vs. Larvae

To estimate seed infestation rates, larval development
time under natural conditions, and the time period during
which endosperm rather than larvae are available in the
endocarps, endocarps were sampled several times during the
study, as follows. On November 15 1996, 61 externally intact
(no exit holes or signs of vertebrate use visible) endocarps
were collected haphazardly from 12 trees that fruited in the
early and peak _Attalea_ fruiting season. They were cracked
with a machete and the size of larvae determined. In
December 1996 ten intact endocarps were haphazardly collected
from all layers of the endocarp piles of the 6 most recently
fruiting trees in the riverine habitat. The percent of
endosperm remaining was estimated for each endocarp. For
endocarps with multiple seeds, the percent remaining of each
endosperm was estimated. In mid-February, 45 intact
endocarps were drawn haphazardly from 9 early and peak
fruiting trees on the eastern forest and riverine habitats.

During the four final checks of endocarp piles (October
15 1996, November 15 1996, December 5 1996 and February 17
1997), an index of bruchid emergence was obtained by counting
the number of endocarps with exit holes on the main endocarp
pile. For approximately 3 minutes the pile was searched by

rapidly turning over endocarps. Endocarps with exit holes
found while searching for mammal-opened seeds were also
collected and counted. During the December count, only a
subset of the trees was sampled. By the time beetles start
to emerge, endocarp piles have often been depleted by
squirrels and agoutis. Data were therefore used only as an
index: no emerged endocarps, emerged endocarps present, and
more than 10 emerged endocarps present (the latter category
indicating a high rate of emergence).

Results

Patterns of Fruit Availability

Eastern terra firme forest. When all fruit and seed
species except _Attalea_ seeds are considered, there were two
peaks of fruit and seed availability between November 1995
and October 1996: one short one in December - January (mid to
late dry season), and one longer one from May through August
(rainy season) (Fig. 4-1). If only "edible" fruits (known or
suspected to be eaten by agoutis, white-lipped peccaries, and
squirrels; Appendix 1) are included, the first peak
disappears. _Attalea_ endocarps were available on the ground
for most of the year, except for March and April, immediately
prior to the new _Attalea_ fruiting season. In terms of numbers
of patches, in this habitat they contributed little to edible

fruit availability, but in terms of timing they were available when other edible fruits were at their annual low.

Due to higher fruiting levels of the palm <u>Astrocaryum aculeatum</u>, <u>Licania</u> sp. (Chrysobalanaceae), and <u>Ecclinusa guianensis</u> (Sapotaceae) in 1996-97 than in 1995-96, a mid-late dry season peak in edible species did occur in 1996-97 in the eastern terra firme forest. The level and timing of fruiting of <u>Attalea</u> was similar in 1995 and 1996. <u>Pouteria surumuensis</u>, however, a species important at least to agoutis and white-lipped peccaries, failed to produce fruit in 1996 during its expected fruiting time (February-May). This was the principal diet item for radio tracked agoutis in 1996 (Chapter 5).

<u>Riverine forest</u>. Fruit and seed availability (number of patches) was lower overall in the riverine forest than in the eastern terra firme forest, but was relatively constant throughout the year, with the exception of a low period in January-February (Fig. 4-2). Edible foods other than <u>Attalea</u> endocarps were scarce, and peaked briefly in May and August. Both peaks were caused by <u>Attalea</u> pulp availability (ripe fruit falling). Thus on the river transect the overall pattern of fruit and seed availability was driven by <u>Attalea</u>. <u>Attalea</u> endocarps were available at all times except March-April, and were most abundant during times when few other edible items were available.

Central terra firme forest. Fruit and seed availability (number of patches) was slightly lower in the central than in the eastern terra firme forest (Fig. 4-3). The same low, short peak in fruit availability as in the east occurred in December-January, and a higher, more extended peak in late April to July, somewhat earlier than in the east. Unlike in the eastern forest, the pattern of edible fruit availability mirrored overall fruit availability. Attalea endocarps contributed even less than in the eastern forest to the edible fruit availability, but were maximally available at the time (August) when other fruits and seeds were scarce.

Combined availability. For all three habitats combined, the period of lowest fruit availability was between February and March, and the period of highest availability was early April to late June (Fig. 4-4). Combining the three habitat types thus shortened the period of apparent fruit scarcity, and shifted it to the end of the dry season.

Attalea Phenology

One hundred and nine fruiting Attalea trees were found along the 15 km of eastern terra firme forest, 77 along the 2 km of riverine forest, and 6 along the 2 km of central terra firme forest. The median length of the fruit drop period was 18 days on the river trail (n= 45 trees with known start and end fruit drop dates) and 15 days on the eastern forest trail

(n = 26 trees). Based on this information, and starting on April 1, the fruiting season was divided into 15 day intervals, and the number and proportion of trees starting to fruit during each interval was plotted (Fig. 4-5a).

The timing of _Attalea_ fruit fall did not differ greatly between the riverine and eastern habitats. The fruiting period was slightly longer and the peak later by about 10 days on the river trail. Not shown on the graph are two trees that fruited on the main trail system in October 1995, and one tree that probably fruited in early April 1996; this would make the spread similar to that of the river trail. The shift to a later season on the river could be due to sampling bias, since the trees there were checked on average three days later than on the main trail, which would affect estimated ages. Sample size for the central forest was too low for comparison, but the six trees that fruited did so within the main fruiting season in the other habitats (Fig. 4-5a).

Endocarp Contents

Beetle emergence. The pattern of emergence was similar in the riverine and eastern forests. Emergence was always gradual, spread over at least a few weeks and more commonly over several months within a single endocarp pile. In October 1996, endocarps at only 19% of all monitored trees showed emergence, and only 2% had more than 10 emerged seeds

(Fig. 4-6). The percentage rose above 40% in November and December 1996, and by February 1997 60% and 80% of endocarp piles respectively showed emergence. The percentage of trees with high emergence rates (> 10 endocarps) at any one time increased slowly, and never overtook the overall emergence rate. The proportion of endocarp piles with beetles of emergence age is probably higher than shown by sampling, since depletion of the endocarp pile by consumers reduces the chance of beetles emerging. Emergence of 10 or more endocarps occurred as early as seed age 71 days, and as late as seed age 265 days. Averaging the age at which endocarp piles first show > 10 endocarps with exit holes, for both riverine and eastern forests, the mean age at first emergence was 121 +/-46.2 days (n = 20 trees).

Endosperm availability. In December 1996, endocarps from three trees that started fruiting 62, 56 and 46 days earlier had an average of 45.2% (+/- 38.1%) of endosperm remaining per seed , and a combined infestation rate of 100%. Three trees sampled at the same time with seed ages 82, 82 and 86 days had only 3.9% (+/- 10.2%) endosperm remaining per seed and a 96.7% infestation rate. The high variation in amount of endosperm remaining exists because there can be a difference of as much as three weeks in the age of the endocarps of a single tree. In addition, oviposition only takes place after the exocarp has been removed, which occurs at a variable rate (Chapter 3). Therefore in a single

endocarp pile both large and small larvae, or even small larvae and adult beetles, can co-occur, and the amount of endosperm remaining per seed can vary from 0 to nearly 100%.

Of the 61 older intact endocarps collected in November 1996, 75.4% were infested with larvae or pupa; 67.2% had large larvae. Of the 45 seeds cracked in February 1997, 91% were infested, and 62% contained large larvae rather than pupae or adult beetles.

Endosperm content was thus greater than larvae content only for endocarps less than 1.5 months old. Since the peak in fruit fall occurred in mid-July (considering the peaks in both areas), the peak in endosperm content should last until late August. Larvae would be maximally available 3 months after the peak, in mid-October. Because endocarps accumulate during the fruiting season, and are only gradually depleted by consumers and beetle emergence, endocarps with larvae remain available into the next rainy season (May).

Endocarp Use by Squirrels, Agoutis, and Peccaries, Eastern Forest

Out of 116 trees monitored in the eastern forest, squirrels fed on 99 trees during the course of the study (at least one endocarp opened), agoutis on 35 trees, and white-lips on 21 trees. A total of 6,801 squirrel-opened, 4,129 agouti-opened, and 258 white-lip-opened endocarps were collected. Squirrels began to open endocarps as soon as the first fruits fell (early May). On the river and central

forest transects, squirrels several times removed large
numbers of pre-ripe fruits from the fruit bunch and opened
them near the tree, removing the exocarp and still firm
mesocarp in strips to reach the endocarp, but this behavior
was never recorded in the eastern forest.

Agoutis did not begin to open endocarps until late June,
and white-lips first cracked endocarps in mid-October.
Agoutis fed on the pulp of Attalea fruits from the time they
began to fall and throughout the fruit fall season (Fragoso
1994, 1997b, Chapter 3, 5). They did not use fresh endocarps,
instead opening endocarps whose mesocarp had already rotted
or been removed several days, weeks or months earlier.

Squirrel and Agouti Use of Endocarps: Temporal Patterns

Squirrels. The proportion of available endocarp piles
used by squirrels peaked early in the season, and then
remained more or less stable (large fluctuations around a
mean) for the rest of the study (Fig. 4-7). The number of
endocarps used by squirrels (weighted by number of days
between checks and number of trees available) increased from
May to August, peaking in late August/early September, and
then declined to pre-peak levels for the last four months of
the study (Fig. 4-8). There were marked fluctuations among
all checks in the number of endocarps opened, perhaps due to
the use of other Attalea trees in the area not included in
the study.

The peak in endocarp use by squirrels, for both % of trees used and number of endocarps opened, occurred prior to the period of low fruit availability. Squirrel use of <u>Attalea</u> endocarps also peaked prior to the period of maximum bruchid larvae availability.

The forest-wide fruit low period coincides with an increase in the availability of <u>Astrocaryum aculeatum</u> fruit and seeds (Fig. 4-9), a favored food of squirrels throughout the Neotropics. In terms of numbers of patches, <u>Astrocaryum</u> did not contribute much to fruit availability; but because the fruits are large (8 cm diameter, second in size only to <u>Pouteria surumuensis</u> in this study) and easy to open, and because infructescences provide between 100 and 200 fruits each, they probably have a major impact on food availability for squirrels.

<u>Agoutis</u>. The proportion of available <u>Attalea</u> endocarp piles used by agoutis increased steadily from late June to late August, decreasing slightly and reaching a plateau between August and November (Fig. 4-7). The number of <u>Attalea</u> endocarps opened increased steadily in July and August and leveled of from September through November (Fig. 4-8). The increase and peak in agouti use of <u>Attalea</u> endocarps coincided exactly with the decrease and low period in availability of "edible" fruits and seeds (August 6 to November 26; Fig. 4-1). The peak in use started prior to and

continued during the period of maximum bruchid larvae availability.

Squirrel and Agouti Use of Endocarps: Spatial Patterns

Attalea trees used by squirrels were spread evenly throughout the eastern forest study site, whereas trees used by agoutis were clumped at the northwest and southeast ends of the site (Fig 4-10). These two areas correspond to high Attalea density, low tree species diversity areas. To the southeast is the "Angico slope" forest type (Milliken and Ratter 1989, 1998); to the northwest a less extensive species-poor habitat located around a Mauritia flexuosa palm wetland embedded in the terra firme forest.

The total number of endocarps used by squirrels at each tree, weighted by the number of days the endocarps were available (start of fruit drop to pile depletion or final check date), was not significantly correlated with the number of either Attalea, Astrocaryum, Pradosia or Pouteria trees within a 25 m radius. For agoutis, the correlation was significant and negative with Pouteria (Spearman-Rank Correlation; r = -2.598, p = 0.0094), and significant and positive with Attalea (r = 4.544, p = 0.001). Thus agoutis used Attalea endocarps only when and where their preferred food, Pouteria surumuensis (Chapter 5) was not available. Squirrels used Attalea everywhere, indicating that it was a preferred food during the study.

Endocarp Use by White-Lips: All Habitats

1995 fruiting season. In the eastern forest, the first
fruit transect was run on November 4 1995. On the second and
third runs (November 20 and December 19) two trees in one
patch had freshly cracked endocarps. No more cracked
endocarps were found on the transect that year, but endocarps
of a tree that dropped fruit in October 1995 and which was
monitored every two weeks for a separate experiment were
found cracked in January 1996. Thus white-lipped peccaries
opened endocarps from mid-November 1995 to late January 1996.

In the central forest, cracked endocarps were first
found on December 21 1995, and freshly cracked endocarps were
again found on January 29 1996. Thus white-lips used
endocarps in this area in December and January, the same time
period as in the eastern forest. On the river trail, a
white-lipped peccary herd was first sighted in mid-October.
The animals were feeding on Attalea endocarps and
Phenakospermum (Musaceae) leaf bases. The first transect in
this habitat was run on November 6 1995. Freshly cracked
endocarps were found on all checks through January 28 1996.
The period of endocarp use on the river trail thus started
earlier than in the other habitats, but ended at about the
same time. The overall period of endocarp use by white-lips
in 1995 was therefore mid-October through late January.

1996 fruiting season. The central forest transect was not checked between October 13 1996 and March 6 1997. During that time period, white-lips opened the endocarps at one of the six trees that fruited in 1996. In the eastern forest, white-lip-opened endocarps were first found at the monitored trees on October 15 1996, and continued to occur on all checks through February 12 1997 (Figs. 4-7 and 4-8). In the riverine forest, white-lip-opened endocarps were first found on November 18 1996 (the previous check occurred on October 15), and continued to be found on all checks through February 17 1997. Thus the period of endocarp use in 1996-97 was nearly identical to that in 1995-96.

White-lips used a relatively low proportion of available endocarp piles in the eastern and central forests (18% and 17% respectively). The trees used on the eastern forest in 1996 (Fig. 4-10) were those located along a traditional travel route that connects two Mauritia palm swamps and one Pouteria patch (pers. obs.). White-lips used this route repeatedly during the study period, and cracked endocarps at the same trees over and over again as they passed through. No tree in the eastern forest ever had as many cracked endocarps as those on the river trail (47 vs. 239), even though the herd that used the river trail was the smaller of the two present in the study area (60 vs. 200 individuals, Fragoso unpublished data). On the river trail, peccaries used 89% of available trees, and visited the area repeatedly (at least every 2-3 weeks) for 3 months (Fig. 4-11). Due to

the dense aggregations of ticks that occur on endocarp piles after white-lip visits, for most trees in February 1997 the number of endocarps cracked was estimated rather than precisely counted. Based on actual counts and estimates, about 5,300 endocarps were opened by white-lips from early November to mid-February on the 2 km river trail.

Endocarp use by white-lipped peccaries thus started later than use by squirrels or agoutis. If across-habitat food availability is considered (Fig. 4-4), white-lip use of endocarps coincided with the low season only in February). Unlike the situation with agoutis and squirrels, endocarp use by white-lipped peccaries corresponds exactly to the period of maximum larva availability.

Discussion

Consumption of Bruchid Larvae

Squirrels, agoutis, and white-lipped peccaries all fed on bruchid larvae to some extent. After November, it was difficult to find <u>Attalea</u> endocarps without larvae, and endosperm content was low even in recently infested seeds. Endocarps incidentally or intentionally buried soon after fruit fall by vertebrates would probably escape infestation, but there was no evidence that consumers other than squirrels dug up previously buried endocarps. Early in the season,

squirrels fed primarily on endosperm from freshly fallen endocarps. As late as November, some seeds opened by squirrels still contained endosperm (in recently fallen fruits, rodents are unable to remove all the endosperm, which is still moist and swollen, and fragments remain visibly attached to the inside of the endocarp). Many endocarps opened by squirrels late in the season were filled with frass, indicating that the squirrel had removed a full-grown larvae rather than endosperm. Frass-filled endocarps opened by squirrels often had a single, small hole per seed, whereas endocarps with intact seeds had larger and sometimes multiple holes per seed. This suggests that it is easier to extract larvae than seeds from the endocarp. The relative energetic value of larvae vs. endosperm is unknown, but the fact that some human communities use them in preference of the seeds suggests that they may be a more digestible source of lipids and other nutrients (Chapter 2; Balée 1988).

Agoutis, by virtue of the time they used endocarps, fed mostly on larva, and frass-filled agouti-endocarps were common. As for squirrels, the effort an agouti expends to open a larva-containing endocarp may be somewhat less than that for a seed-containing endocarp, especially since larvae thin away the endocarp by scraping from the inside.

Both rodent species, however, essentially have to carve through a fixed endocarp thickness to reach the contents. White-lipped peccaries, on the other hand, open the endocarps by snapping the jaws shut. A hollow object is easier to

crack in this way than a solid object, and a larvae-
containing endocarp is essentially a hollow object. When
seeds were cracked with a machete, infested seeds broke on
the first strike, while intact ones required several strikes.
Other observations suggest that endocarp thickness may be a
limiting factor for peccaries. Fragoso (1994) found that
white-lips are unable to crack the thickest _Attalea_
endocarps, whether or not they contain larvae. P. Crawshaw
(pers. com.) reports finding two skulls of white-lipped
peccaries where _Attalea_ spp. endocarps embedded in the palate
had apparently killed the animal. White-lipped peccaries may
thus be able to use _Attalea_ endocarps only at the time of
maximum bruchid infestation.

Infestation by bruchids may thus actually increase
endocarp quality for consumers usually classified as
granivores, and provide an abundant source of protein and
lipids. It is not surprising that Neotropical squirrels
should feed on bruchid larvae, given the degree of
insectivory reported for temperate (Davis 1907, Steele et al.
1996) and Old World tropical (Emmons 1980) squirrels, and the
ability of at least temperate zone squirrels to distinguish
between infested and non-infested seeds (Steele et al. 1996).
Insectivory by agoutis is not as well documented, but several
researchers report use of animal matter. In Mexico, 94% of
18 fecal samples contained insect parts (E. Naranjo and J.
Croker, unpublished data), and agoutis were observed feeding
on vertebrate eggs, juveniles, and adults. In southern

Brazil, captive agoutis readily killed and ate domestic chicks. (C. Castellano-Margarido pers. comm.), while Smythe (1978) predation on a _Liomys_ by a captive agouti. That agoutis at the Maracá study site do not hoard _Attalea_ endocarps may be partially a result of a preference for infested seeds over uninfested ones, although the abundance of the endocarps probably also obviates the need for hoarding.

Spatial and Temporal Pattern of Endocarp Use

The three consumers studied used _Attalea_ endocarps in very different ways. The northern Amazon red squirrel, as expected from its known specialization on palm seeds (Chapter 2), fed on endocarps year round. Agoutis used endocarps during the season of food scarcity, but only in specific microhabitats where preferred seeds were not available. White-lipped peccaries visited certain macrohabitats (forest types) specifically to feed on _Attalea_ seeds: there are no other fruits besides _Attalea_ available on the river trail in sufficient quantity to feed a large herd of white-lips.

The fact that white-lips were feeding on difficult to obtain food (hard endocarps) and a probably low nutrient food (_Phenakospermum_ leaf tissue) at the same time suggests that they were feeding on non-preferred, low value foods. On the other hand, the fact that they used _Attalea_ palm endocarps during the time when bruchid larvae, a high-energy food, were

maximally available (large numbers, and easy to open),
suggests that Attalea endocarps were being used as a
preferred food. A consideration of patterns of food
availability weighs in favor of the second possibility.

For agoutis, the time of food scarcity was probably
adequately monitored by the 2-kilometer transects. Palm
wetland habitats were not monitored in this study, but they
may be relatively unimportant as many agoutis in the terra
firme habitats do not have access to this habitat (Chapter
5). The simultaneous radio-tracking study (Chapter 5)
indicated that for agoutis Attalea palms are not a preferred
food; four agoutis tracked in terra firme forest along the
phenology transect never fed on Attalea seeds, although they
used Attalea pulp heavily. Agoutis relied instead on seeds
in the Sapotaceae.

For white-lipped peccaries, fruit availability was not
adequately measured by the three transects, even when data
from the three habitats are combined. White-lips rely
heavily on Mauritia swamp habitats for palm pulp, seeds, and
seedlings, and for invertebrates. At the end of the dry
season, they may congregate at pools to feed on fish left
stranded as the water recedes (Fragoso 1994). They move over
huge home ranges incorporating many macro (several kilometers
in extent) and micro (several hundred meters or less in
extent) habitat types (Fragoso 1994, in review). The two
herds that visited the study in 1995-97 moved up to 20
kilometers from any one of the three transects (Fragoso

unpublished data). It would be difficult to monitor food availability simultaneously across their home range. Overall, they used <u>Attalea</u> in the scarcity season for the three forest types monitored on Maracá--the mid-dry season. However, this is also the time on Maracá when wetlands are beginning to dry and food is plentiful in the form of fish and germinating seeds. It is therefore unclear whether for an animal operating at a large scale habitat mosaic, the season of low fruit-production in one or a few habitats can be considered a season of food scarcity.

For agoutis in the eastern forest, <u>Attalea</u> could be interpreted as a non-preferred, season of scarcity resource. Some <u>Attalea</u> trees that were not used by agoutis during this study period had endocarps opened by agoutis during the 1994 season. In years when preferred foods fail, as did <u>Pouteria</u> in 1997, agoutis may thus rely more heavily on <u>Attalea</u> endocarps. Smythe et al. (1996) found a similar pattern with use of <u>Attalea</u> endocarps by agoutis on Barro Colorado Island, Panama.

The differences in the ecological relationships between these three consumers and <u>Attalea</u> suggests that they will react very differently to environmental fluctuations; i.e., changes in food availability will lead to individual, species-specific rather than community level, changes in <u>Attalea</u> endocarp use.
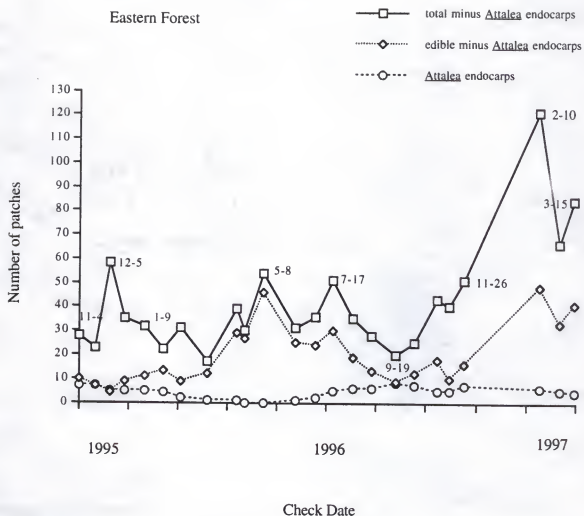
Figure 4-1. Contribution of _Attalea_ endocarps to total and edible fruit and seed availability on the eastern terra firme forest transect.
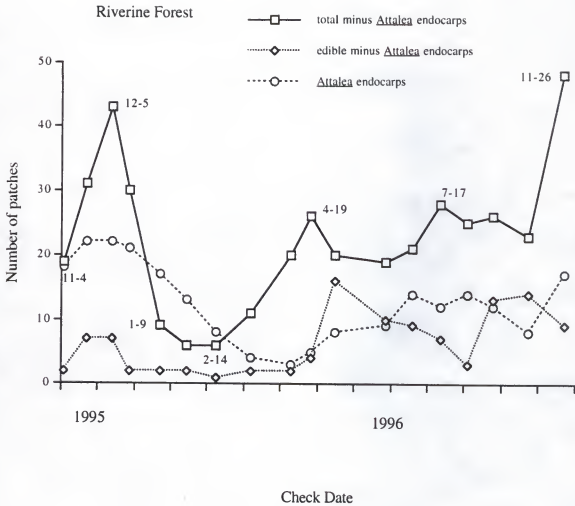
Figure 4-2. Contribution of __Attalea__ endocarps to total and edible fruit and seed availability on the riverine forest transect.
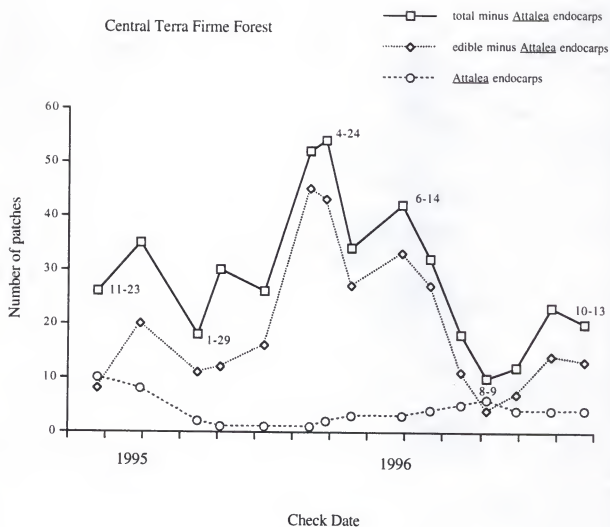
Figure 4-3. Contribution of _Attalea_ endocarps to total and edible fruit and seed availability on the terra firme forest transect.
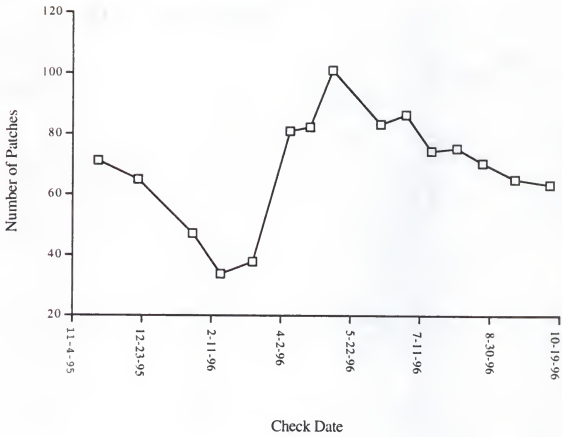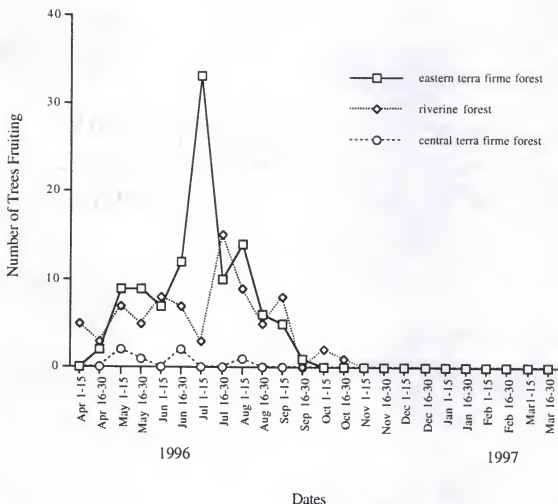
Figure 4-4. Fruit availability summed across all three forest
habitats (eastern terra firme, central terra firme, and riverine).

a)

Figure 4-5. Timing of fruit production by monitored <u>Attalea</u> trees along a 2 km long trail in each of three forest types. a) Number of trees that started fruiting during each two week period from April 1 1996 to March 30 1997. b) Percentage of trees monitored that started fruiting during the same period.
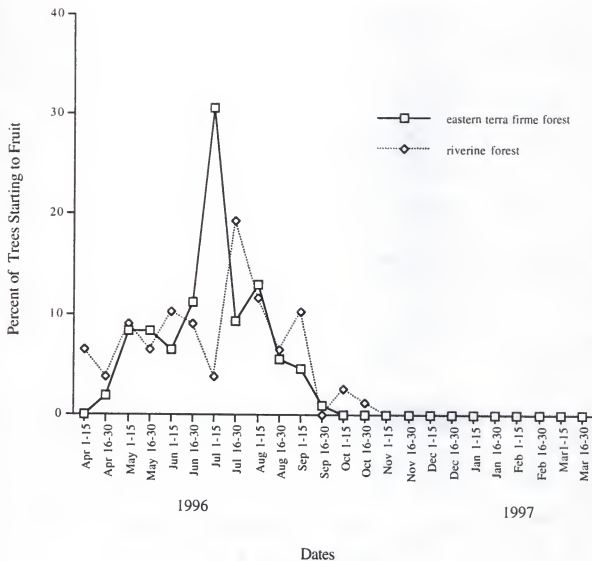
b)

Figure 4-5, continued.
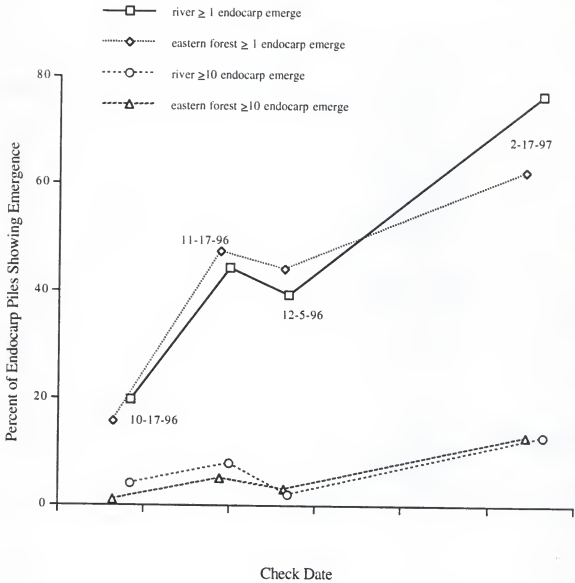
Figure 4-6. Bruchid beetle emergence from <u>Attalea</u> endocarps in the riverine and eastern terra firme forests. > 1 endocarp includes all endocarp pile with at least one exit hole; > 10 endocarp includes only those with at least 10 exit holes, indicating a high rate of emergence.
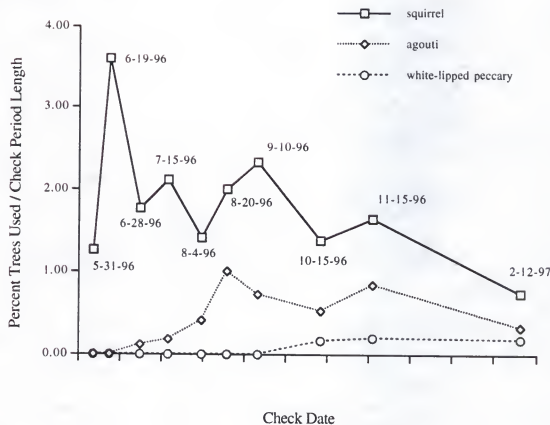
Figure 4-7. Proportion of available endocarp piles used by each of the three study animals in the eastern terra firme forest during each monthly check period from May 31, 1996 to February 17, 1997.
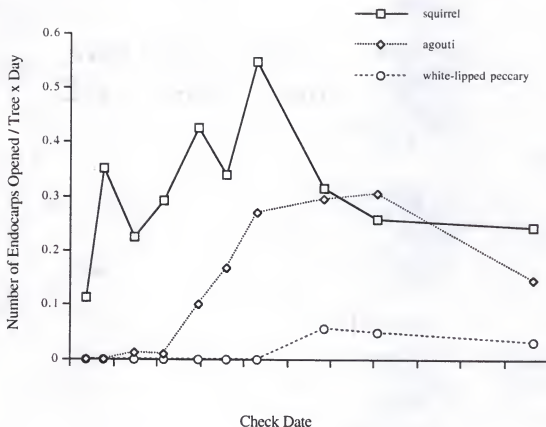
Figure 4-8. Number of endocarps opened by each of the three study animals in the eastern terra firme forest during each monthly check period from May 31, 1996 to February 17, 1997, weighted by the number of days endocarps were available between consecutive checks. Dates on x-axis as in Figure 4-7.
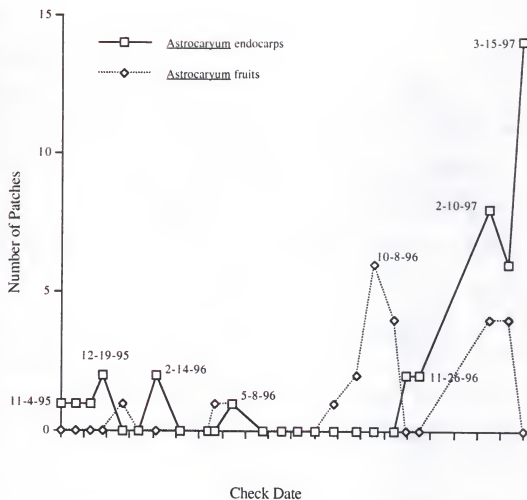
Figure 4-9. Availability of <u>Astrocaryum</u> <u>aculeatum</u> fruits and seeds on the eastern terra firme forest trail (Trail 2) from November 1995 to March 1997.
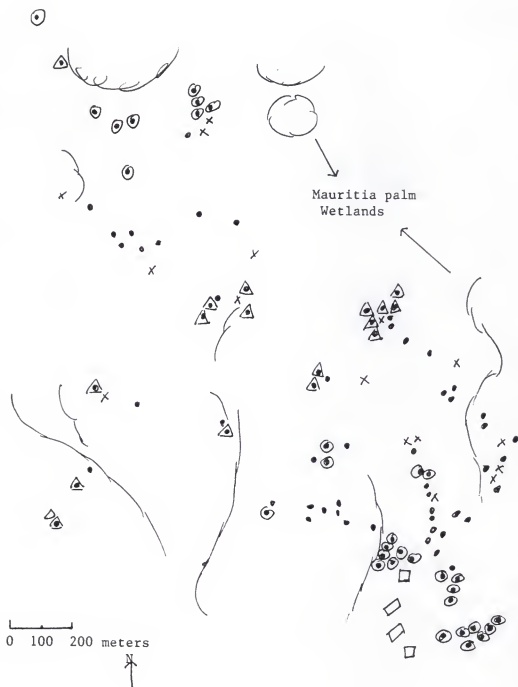
Figure 4-10. Location of endocarp piles used by each of the three study animals for the eastern terra firme forest monitored _Attalea_ population. (•) = _Sciurus igniventris_; (o) = _Dasyprocta agouti_; (Δ) = _Tayassu pecari_; (x) = not used by any consumer.
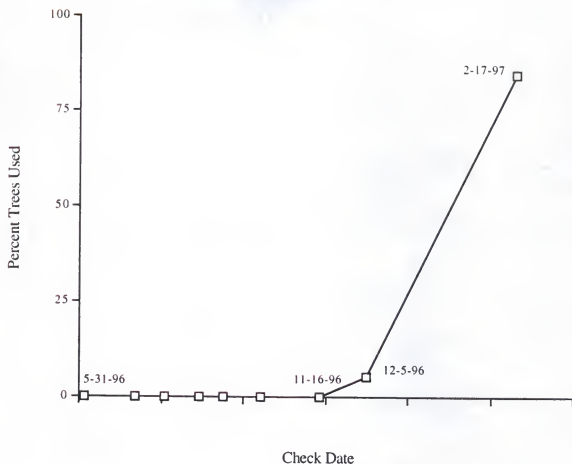
Figure 4-11. Proportion of available endocarp piles used by white-lipped peccaries on the riverine forest trail during each monthly check period from May 31, 1996 to February 17, 1997.

CHAPTER 5
AGOUTI (<u>DASYPROCTA</u> <u>AGOUTI</u>) HABITAT USE, DIET AND HOME RANGE
ON MARACÁ ISLAND ECOLOGICAL RESERVE, NORTHERN BRAZILIAN
AMAZON

Introduction

Agoutis are large terrestrial rodents (2-5 kg),
ubiquitous in Neotropical dry and moist forests. Eleven
species range from southern Mexico to northern Argentina
(Emmons and Feer 1997). Male-female pairs defend a territory
and share it with their young until these reach reproductive
age and disperse (Smythe 1978). Although territories are
well-delimited and agonistically defended, animals from
several territories will come together to feed at a
super-abundant food source such as a large fruiting tree or a
bait station (Smythe 1978, Silvius pers. obs.). Such
behavior suggests the social system could be flexible enough
to shift with changing population densities and resource
levels.

Agoutis are primarily granivorous, but also eat varying
amounts of fruit pulp, leaves, fungi, and animal matter.
Throughout their range they interact with large seeds in the
Leguminosae, Palmae, Sapotaceae, Lecythidaceae, and
Chrysobalanaceae (Smythe et al. 1986, Hallwachs 1986, Allen

1997) but also with smaller-seeded species in the
Myristicaceae, Moraceae and Burseraceae (Forget and Milleron
1991, Wenny 1998). They are reported to hoard some species
of seeds when these are abundant on the forest floor (i.e.
during ripe fruit fall), and to rely on them for food during
seasons when they are less abundant (Smythe 1978). Hoarding,
however, is habitat and season dependent (Forget and Milleron
1991, Smythe 1978).

Only one published study of agouties obtained home range
sizes, from visual observations and trapping (1-2 ha, moist
tropical forest in Panama, Smythe 1978). There are no
published studies of radio-tracked agoutis, although papers
on studies in Mexico (E. Naranjo, pers. comm.) and Colombia
(O. Montenegro, pers. comm.) are currently in preparation.
Approximate home range sizes are reported from two additional
studies, but the methods by which they were obtained are not
described (200 meter diameter area, rain forest in French
Guiana, Dubost 1988; 4-6 ha in regenerating Costa Rican dry
forest patches, Hallawachs 1986). Reported population
densities range from 1 to 63 animals per km^2 under free-
ranging conditions; the reasons for these differences have
been examined only in light of the role of predators in
controlling agouti populations (Wright et al. 1994).

This paper reports on the natural history of an agouti
(Dasyprocta agouti) population with respect to diet, habitat
use, home range size, and seed handling. Five agoutis were
radio tracked in the transitional forest between the Rupununi

savannas and the Amazon rain forest as part of a study on palm use by Neotropical terrestrial frugivore-granivores. The primary purpose of the tracking effort was a) to estimate the scale at which agoutis respond to fruit distribution (individual fruit, individual tree, tree patch, or habitat) and b) to describe the role of the palm _Attalea maripa_ in their diet. Radio-tracking secondarily provided information on home range size, seasonal changes in foraging patterns, dietary composition, and seed handling behavior. I use these observations to discuss the relative importance of plant distribution patterns, predation, and competition on agouti home range sizes and population densities.

Study Area

Research was carried out on the main trail system on the eastern tip of Maracá Island Ecological Reserve, Roraima state, Brazil. The Reserve and surrounding area have been described in detail in Milliken and Ratter (1998). The core trail system of about 40 kilometers in a 2 x 3 km area was established by Moskovits (1998) for a study of tortoises (_Geochelone_ sp.). It was used again by Nuñes (1992) for a study of spider monkeys (_Ateles belzebuth_), and expanded by Fragoso (1994) in a study of collared (_Tayassu tajacu_) and white-lipped peccaries (_T. pecari_). Approximately 60 kms of trail were included in this study (Fig. 5-1).

Rainfall records on the eastern end of the island show variation between 1750 and 2,300 mm annually; during El Niño years, rainfall decreases markedly across the state. The wet season is between May and September, the dry season between October and April, with rains starting either in early or late April. The heaviest individual rains tend to fall in the dry season. During the study period covered in this paper (July 1996 to March 1997), rainfall conformed to the modal seasonality.

Floristics on Maracá are described in detail in Chapter 6. The most abundant large seeded tree species are primarily in the Sapotaceae and Palmae, and secondarily in the Leguminaosae and Lecythidaceae. Sixteen species of palm and 16 of Sapotaceae occur on the island, with _Attalea_ _maripa_ and _Astrocaryum_ _aculeatum_ the most common terra firme palms, and _Pradosia_ _surinamensis_, _Pouteria_ _surumuensis_, _P._ _venosa_, and _Ecclinusa_ _guianensis_ the most common species in the Sapotaceae.

Two studies of plant reproductive phenology on the trail system (Moskovits 1985, Nuñes 1992, 1995) indicate that peak forest-wide (all species) ripe fruit availability on the canopy occurs in the mid-to-late rainy season. Based on the proportion of trees sampled producing ripe fruit Nuñes (1992) detected a peak from May through July, with high availability extending into September. Moskovits (1985), using counts of fruits on the canopy, detected peak fruit availability in May through June, with a marked decrease in August and September,

lowest levels in October to December, and a gradual increase
in January through April.

Methods

Radio-Tracking

Agoutis were captured with agouti-hunting dogs trained
by local Macuxi Amerindians. Hunter and dog walked through
the forest until the dog gave chase to an agouti, which
invariably ran into a hollow log. The dog stayed by the log
until the hunters arrived. The agouti was extracted by
cutting open the log or inducing the animal to run toward the
opening, where it was caught in a bag. It was immediately
mildly anesthetized with 3.33 mg/kg of Telazol (Tiletamine
hydrochloride + Zolazepam), weighed, radio collared with a
Telonics® model radio collar, and replaced in the log to
recover from sedation.

A few days after the capture, the animal was located by
radio and all the pre-existing trails potentially within its
home range marked at 25-meter intervals. Subsequent
locations were made by a) determining the general location of
the animal from outside its home range (signal strength was
an indicator of distance) and b) subsequent triangulation
from the marked trail locations, usually at 50 meter
intervals. Approaches to the home range were varied between
tracking sessions, to avoid site-specific biases in radio

signals. All bearings taken were immediately marked on a trail map. Because the tracker was very close to the animal (usually $\leq$ 25 meters for final triangulation), error triangles were small unless the animal was moving. If the animal was moving, it was tracked until a good triangulation was obtained. If it was moving very rapidly, and did not settle down within 20 minutes, tracking was stopped. Locations in these cases were included in the home range calculation, but no habitat description (below) was carried out.

After a satisfactory location was obtained, the tracker walked a compass bearing to the location, searched for food items or signs of activity, and described the habitat according to the parameters listed below. Because the tracking method was intrusive, three days were allowed to elapse between tracking sessions in order to minimize disturbance to the animal. After the first few days of tracking, when they occasionally "stalked" or walked parallel to the tracker, the animals gave no indication of being disturbed by the tracker. They never startled or gave alarm calls, and usually remained at the site of the first location. Five animals were tracked between July and December 1996, and one of these continued to be tracked in February-March 1997.

Because the main purpose of radio tracking was to examine habitat use during foraging, the animals were tracked at those times when they were most likely to be foraging

rather than patrolling or resting: between 0830 and 1100 in
the morning, and between 1430 and 1730 in the afternoon
(sunrise and sunset were at 0600 and 1800 respectively).
The choice of times were based in information in Smythe
(1978), modified by the results from initial tracking
sessions. Twelve-hour daylight follows on Maracá confirmed
that between 0600 and 0800 the agoutis moved rapidly between
widely separate points in their home ranges, suggesting
patrolling activity. By 1100 hours, they were often moving to
or already at preferred resting areas in recent treefalls.
Tracking sessions on individual animals were alternated
between morning and afternoon, so that both times were
equally represented for all individuals. Animals were not
tracked during heavy rainfall, but all other weather
conditions were represented.

On 10 occasions, agoutis were tracked from about 0600 to
1800 ("twelve hour follows"), with radio locations every half
hour or every hour, to confirm movement patterns and home
range use. Locations were not inspected or habitats
described during these all day follows, except on three
occasions when they were used to augment the data set and the
animal had not been tracked within three days of the session.

Habitat Description at Location

Food eaten and available. The ground within a 5 m radius
of each accurate radio-location was searched for partially

eaten food items or signs of digging and all fruit or seeds
were noted. A distinction was made between "eaten" foods,
those that had bite marks on them or were associated with a
hole or scrape mark or regular feeding area (a cleared area
on the ground with food items around them), and those that
were "available," that is, in the immediate area were the
animal had been but not eaten or associated with foraging
signs. If an "eaten" item was clearly not fresh, but had
been used within the last three days, it was still recorded.

Presence of focal tree species. The observer
qualitatively determined whether the location was within a
patch of one of four large-fruited (5-20 cm diameter) tree
species important to seed-eating animals in the study site:
Attalea maripa, Astrocaryum aculeatum, Pradosia surinamensis
and Pouteria surumuensis. A location was considered to be
within a patch if trees of the focal species completely
surrounded the location, with at least 3 trees within 10
meters.

Agouti Encounter Transects

In March, April, May, July, and August 1996, an
experienced Macuxi tracker walked on 86 occasions through
different parts of the trail system. He noted all mammals
seen, including agoutis, and described their behavior. If
the animal was feeding he identified the food item. All

trails were covered every month, and sometimes every week.
The walks lasted usually from 0730 to 1130, and from 1345 to
1715.

Use of Attalea Endocarps

Use of Attalea maripa endocarps by agoutis was monitored
on a monthly schedule on the trail system (see Chapter 4 for
detailed methods). For Attalea palms that fruited within the
radio-tracked agoutis' home ranges, all endocarps opened by
agoutis within a 5 m radius of the trunk were counted and
removed.

Phenology

A 2 km long by 3 m wide transect on a pre-existing trail
that runs through or between all the marked agouti
territories was walked at 2-3 week intervals from November
1995 through March 1997. All fruits and seeds seen on the
ground were counted and identified, with each individual item
or cluster of items counted as a single patch. Both ripe or
newly fallen items and older seeds that remained on the
ground, sometimes for months, were counted, and their stage
identified (immature, preripe (full size but immture color),
ripe, rotten, and germinating). If the items showed signs of
having been fed on (tooth marks, disturbance, or fruit
fragments), the most likely consumer was noted (e.g.,
tortoises as well as agoutis fed on Pouteria seeds, but their

larger "beak" marks could be distinguished from rodent tooth marks, as could the irregular seed fragments left behind).

The ground monitoring method was chosen for three reasons: a) agoutis can only feed on fruit that falls to the ground; b) because there is a delay in the availability of food items to terrestrial frugivore/granivores compared to arboreal consumers (Zhang and Wang 1995); and c) because agoutis feed on older seeds and germinating seeds whose availability would not be measured by canopy observations or fruit trap sampling. Because fruits are rapidly removed by terrestrial animals (Zhang and Wang 1995), a patch based enumeration was used rather than individual fruit counts, and no attempt was made to estimate the total number or mass of fruits and seeds falling to the ground. Fallen fruit were used as an index of the overall pattern of fruit availability. Although ground transects may fail to capture some fruit species that fall to the ground in low numbers (Zhang and Wang 1995), because agoutis feed on large fruits for which remnants of feeding can be found and counted, this error was minimized. To avoid disturbing the agoutis whose home ranges overlapped the transect, the ground was not raked nor the counted fruits removed.

The number of a) patches and b) species of fruits and seeds considered to be usable by agoutis was plotted for each transect sample (Appendix I lists the species considered). For <u>Pouteria surumuensis</u>, <u>Attalea maripa</u>, <u>Astrocaryum aculeatum</u>, and <u>Pradosia surinamensis</u>, the availabilities of

unripe, ripe, or rotting fruit, and old intact seeds were
plotted individually.

Data Analysis

Because all animals occupied similar habitat types, and
all had roughly equal amounts of the four focal tree species
available to them, data from all animals were combined for
habitat analyses to increase sample size.

The initial intention was to compare the habitat
descriptions of agouti locations with randomly chosen
locations within the home range of each animal. However, the
home ranges were so small, and the locations so near to each
other, that this proved impracticable. Instead, all
locations from July to December were plotted on a single map
for each animal. The three areas with highest density of
locations ("cores"), and the three areas with lowest density
of locations ("holes"), each with at least a 25 m radius,
were selected visually from the maps. The core and hole
areas were then located on the ground, and all reproductive
size individuals of each of the four focal tree species
located within 25 meters of the estimated center point were
counted. The number of canopy gaps and hollow logs in the
area where also counted, as these are two other variables
that could affect the presence of agoutis. Center points
were located by measuring the distance on the map along a
bearing from a 25 m mark to the center of the hole or core

area, and then walking this distance along the bearing in the field. Data on the hole and core areas of all the animals were combined, and the number of trees of each of the focal species compared with a Mann-Whitney U test.

Trees of the four focal species were counted along the 2 km x 3 m fruit availability transect. Their frequency of occurrence was compared with a Chi-Square test to the frequency of the same species in a forest inventory plot in the same area (Milliken and Ratter 1989). Since there was no difference between the two distributions, the relative frequency of trees of the four species on the transect was compared to the frequency with which radio tracked agoutis were located in a patch of each of the four tree species.

Home Range Calculations

Home range size was calculated using the program Wildtrak® (ISIS Innovation Ltd. 1993). Exact locations on the field maps were translated to coordinates on a 7.9 m grid and the coordinates were entered in the program. 100% contour lines were used (i.e., all locations on the boundary of the range were included) because, due to the non-traditional tracking protocol described above, locations were considered minimum indicators of home range size. All locations, including repeat locations during single tracking sessions, and those obtained during all-day follows, were used for home range size calculations. Seasonal shifts

within a home range, however, are depicted using only the
first location from each tracking session, and locations from
all day follows are not included.

Results

Captures and Survivorship

Six female and two male agoutis were captured between
February and August 1996. Only one male and four female
agoutis are included in this study. Individual agoutis were
tracked for between 2 and 6.5 months, during the mid to late
rainy season (July to November, 5 animals), and the dry
season (February and March, 1 animal). Variation in length
of period tracked was caused by death of animals and radio
failure at different times. A total of 197 locations with
habitat descriptions were obtained (Table 5-1). Each animal
is henceforth identified by its radio frequency.

Female 167 was found dead on November 23 1996. She had
been killed the previous day, and had been tracked the day
before that. The collar, still around the body, showed sharp
bite marks, and the antenna was twisted by chewing,
suggesting predation by an ocelot (_Felis pardalis_). When the
study was interrupted in the first week of December, the
other four animals were still alive. In the first week of
February, when the study was resumed, the signal for Male 148

could not be located. That radio had been active for the
longest period of time (ten months) and the batteries had
probably failed. The radios for Females 158 and 170 were
found with bite marks like those on 170, but no animal
remains were associated with them. One radio was adjacent to
a preferred denning site, the other had been carried into
tangled undergrowth in a <u>Mauritia</u> palm stand outside the
known home range of the animal. The lack of smell and
remains, together with the condition of the collars,
suggested the animals had been dead for at least 2 or 3
weeks. The fifth animal, Female 163, was still alive at the
end of the study, 9 months after it had been radio collared.
One female radio collared in February 1996, but not otherwise
included in this study, was found dead and partly
decomposed/scavenged in March, with no tooth marks on the
collar or other signs of predation. The period from November
to January, when animals 167, 158 and 170 died, corresponds
to the mid-dry season and also the season of lowest fruit
availability.

<u>Diet</u>

     Food items with agouti teeth marks or associated with
agouti signs were found within a 5 m radius of the location
at 140 out of 197 radio locations that were checked.
     During 86 walked transects from March 7 to August 30
1996, agoutis were encountered 152 times and 29 feeding

observations were obtained. Eight items were recorded during
casual observations, four of these from exotic plants planted
near the research station buildings.

Thirty eight food items from 19 wild and 4 cultivated
plant species in 11 families were identified (Table 5-2).
Plant parts included, in order of importance: seeds, pulp,
cotyledons, leaves and flowers. In addition, agoutis also
fed on bruchid beetle (Pachymerus cardo: Bruchidae) larvae
from palm nuts and on fungi. The most frequently eaten
species during radio locations were Pouteria surumuensis
(29.3%) and Pradosia surinamensis (20.7%), both in the
Sapotaceae, and Attalea maripa (12.9%), in the Palmae. For
the two Sapotaceous species only the seeds were eaten, while
for the palm the pulp was the item most frequently eaten.
During the mammal transects, Pouteria and Attalea were also
the most frequently eaten items (74% and 22%, respectively),
but Pradosia was not noted. The fruiting periods for
Astrocaryum, Licania sp., Couepia sp., and Licania
kunthiana, the next most frequently noted species in radio
locations, did not coincide with the transect period.

Use of Attalea maripa Endocarps

Female 163 had the highest density of Attalea palms in
her home range. Five trees dropped fruit prior to or during
the radio tracking study (6-20-96 to 9-1-96). Agouti-opened

endocarps were first noticed at two trees in early September 1996 (Table 5-3). Four trees had opened endocarps when checked in mid-October; and all five in mid-November 1996. In mid-February 1997, all trees again had agouti-opened endocarps. Peak endocarp use occurred in November through January (6.17 to 4.62 endocarps per day). On the tree most heavily used between November 1996 and February 1997, many of the opened endocarps were lying around a cleared area on the ground typical of agouti feeding sites (Smythe 1978).

The remaining agoutis had at least between one and five fruiting <u>Attalea</u> trees within their home ranges. No endocarps were opened by agoutis at any of these trees during the radio tracking study or by February 1997.

Hole-Core Description

Core areas had a significantly higher number (Mann-Whitney U, p = 0.007) of <u>Pouteria</u> <u>surumuensis</u> trees (3.36 +/- 1.7) than did hole areas (1.57 +/- 1.34) (Table 5-4). All other parameters were virtually indistinguishable between hole and core areas, except that there was a non-significant tendency for hole areas to have more large gaps (Table 5-4).

Patch Choice

For the July through December observations, there was a significant difference between the frequency of agouti

locations within patches of each of the focal trees and the frequency of the occurrence of focal trees along the transects (X^2 = 7.95, p = 0.05) (Table 5-4). Agoutis were more likely to be found near <u>Pouteria</u> patches and less likely to be found in <u>Attalea</u> patches than expected.

Phenology

With the exception of July, most of the agouti radio tracking study coincided with the usual environmental period of decreasing or low fruit production in the study site. The availability of species considered usable by agoutis in this study (Appendix I) followed the same general pattern found in the previous studies, but the pattern was more marked for the number of fruit and seed patches (Fig. 5-2a) than for the number of species of fruit (Fig. 5-2b) available. The much higher availability of species and patches in early 1997 than in early 1996 was due to heavy fruit production by two species in the Sapotaceae, <u>Pouteria</u> <u>venosa</u> and <u>Pouteria</u> <u>hispida</u>, and one palm, <u>Astrocaryum</u> <u>aculeatum</u>. The latter had a weak fruiting season the previous year, and the two former species aborted all their fruits at the immature stage in 1996 due to heavy insect infestation.

The four core species used by agoutis had disjunct fruiting patterns. <u>Attalea</u> palms began to drop ripe fruit in late April, peak fruit production occurred in June-July, and some trees produced fruit until September (Fig. 5-3). The

endocarps remained on the ground into the next year; in fact, _Attalea maripa_ endocarps are plentiful on the ground all year except for the four months (February-May) prior to and during the start of the fruiting season.

Pouteria surumuensis (Fig. 5-4) did not drop ripe fruit until March, but preripe fruits with edible seeds (as indicated by agouti use) were available from January, and bare seeds with the pulp removed or rotted were plentiful on the ground until August. After that, most of the seeds found on the ground were partially eaten, germinating, or partially rotten.

Tracking and transect observations were interrupted in December 1995 - January 1996. This was the time when _Astrocaryum aculeatum_ ripe fruit was maximally available (Fig. 5-5), and it probably formed an important part of the agouti diet at that time, based on the number of seeds cleared of pulp and gnawed open that were found in February. Seeds remained abundant on the ground into April, when the study ended.

Unlike the above species, _Pradosia surinamensis_ germinated very quickly after falling and was available for a short time as germinating seeds (Fig. 5-6). Heavy use by primates limited the fall of ripe fruit in this study area, though a few kilometers away more ripe fruit was available. In fact, most of the fruit that fell to the ground had been opened by primates, which fed on the pulp and dropped the seeds. _Pradosia_ also had an irregular to biannual fruiting

cycle, so that although seeds were available for short
periods of time, they were produced frequently. Agoutis fed
heavily on the seeds when they were available.

When the fruiting patterns of the four primary food
species are combined (Fig. 5-7), the period of maximal fruit
availability occurred from May to August, with a second peak
induced by Astrocaryum and Couepia sp. in January-March.
Agoutis were already feeding heavily on Pouteria in March
1996, based on the transect observations. Pouteria was
abundantly available since January, and the first agouti-
gnawed seeds and fruits appeared in February during the
phenology transect. Agoutis continued to feed on Pouteria
throughout the tracking period, to the end of November, at a
fairly similar rate, indicating that they were feeding on
buried seeds. The proportion of observations on Pouteria was
lowered by data on the one agouti, Female 163, that had low
availability of these fruits in its territory. Thus, agoutis
used a single food item for nearly the entire year, and
relied on it heavily for at least 7 months (February-August).

Seed handling

Pradosia surinamensis. Agoutis always removed the
endocarp and seed coat on all stages of Pradosia seeds. They
foraged frequently among the germinating seedlings, uprooting
them, but no evidence was found that cotyledons were being
eaten. In one case, three clipped seedlings were found with

only the root remaining, suggesting that the stem and leaves
were eaten.

   Pouteria surumuensis. Initially, intact fruits or
fruits with the entire seed removed were found on the
phenology trail, with no evidence of seeds being eaten on the
spot, suggesting they were being hoarded. By July, many seed
chip piles or seed coat piles were found at these same sites,
indicating that the seed was being manipulated prior to
removal (seed coat removed) or eaten on the spot (seed
chips).

   Pouteria seeds began to germinate about a month after
ripe fruit drop. Some seeds left above ground developed a
green layer under the seed coat, and these were ignored by
the agoutis, which appeared to prefer white seeds. Several
observation of germinated seed and seedling handling from
July 1996 to March 1997 suggest that in addition to burying
seeds for storage, agoutis were removing germinated tissue
from *Pouteria* seedlings, without feeding on the seed at the
time the seedling was cut. In three cases, seeds were dug up
or partly eaten that had obviously had their roots and stem
clipped at least once before and had then been reburied. In
one case, the agouti clipped the stems of two seedlings in a
clump of eight seedlings, without digging up the seeds. In
two cases the seeds were dug up and removed/eaten from
seedlings, with the stem remaining in the ground. In one
case, the agouti was startled away from the seed just after

clipping the seedling. In another, it had been digging at the base of the seedling and was startled before reaching the seed. In one case, the agouti dug up the seed, clipped it away from the seedling (root and stem remained in ground) and had a hole 45 cm away where it was about to bury the seed when startled. The seed oozed plentiful milky sap where it had been cut. Foraging near <u>Pouteria</u> trees was thus not limited only to finding, eating and burying seeds.

Core Area Use and Observed Movements with Respect to Fruiting Trees

Movements and core areas of the radio tracked animals were strongly influenced by 1) the location of individual fruiting trees, and 2) the location of logs or tree-falls or areas of tangled branches/vines. Agoutis tended to forage near one or two <u>Pouteria</u> trees at a time during a period of from a few weeks to two months, creating within their home ranges a pattern of core areas centered on these trees. In several cases, and especially late in the tracking period when <u>Pouteria</u> seeds had been depleted, core areas focused on trees of other species (e.g., <u>Licania kunthiana</u> for Female 170, <u>Couepia</u> sp. for Female 163). Distances between fruiting trees of all species were large enough to create distinct concentrations of locations on the maps. Because fruit species were available at different times, the shift of agoutis from one core tree to another created a seasonal shift in the area of the home range most heavily used.

Figures 5-8 through 5-12 show these seasonal shifts when the tracking period for each animal is divided into two approximately equal time periods.

In several instances preferred feeding trees were associated with shelter areas. Thus Female 158 (Fig. 5-8) fed consistently on a _Pouteria_ tree in the eastern portion of its range, and sheltered in a large hollow log adjacent to it. When seeds were depleted, she started to use a _Pouteria_ patch on the southern boundary of her range, where she was once chased by a neighboring agouti. Although seeds had been available there all along, she did not shift to that area until November.

Observations of the one agouti that was tracked across a change of season, Female 163 (Fig. 5-12), shows that this season shift extended into three different periods of fruit availability. Her home range use pattern also suggests that the fringe areas of the home range, as well as unused areas in the center of the range ("holes"), may be heavily used at other times of year as different trees come into fruit. Two areas that had previously been unused became centers of activity in November and February, due to the presence of fruiting _Couepia_ sp. and _Tetragastris panamensis_ trees.

The use of preferred shelter areas affected the core area pattern. For Female 163, the heavy use of the area near the 50 meter mark on the clearing edge is due to the presence of a vine tangle where the agouti sheltered her young. The young animal was subsequently found dead near this area. On

this and one other occasion when an agouti had young, its movements became very restricted for about two weeks, focusing on a shelter area. Prior to a range shift in October-November Female 167 (Fig. 5-9) used a den in August in the southern part of her range, even though the rest of her activities were concentrated to the north. During one all day watch, this female did not move more than 50 meters from the den site.

With the above exception, locations obtained during all day watches usually covered one half to two thirds of the animals' previously known home ranges, and at most extended the known range by 10 or 20 meters, without adding completely new areas (Table 5-6, Figs. 5-13 through 5-15). During a single day the animals spent most of their time in one or two areas, with occasional movements to the edges of their range once or twice a day.

Only one agouti, Male 148, had a _Mauritia flexuosa_ palm wetland in its home range, and it began to use that area when _Mauritia_ was dropping flowers and immature fruit. This animal and one other had large _Licania kunthiana_ trees in their home ranges, and both changed their movement patterns at one time to use them. Male 148 had _Attalea_ seeds available in its preferred _Pouteria_ core area, but never used them--there were no gnawed seeds and no sign of digging. When _Hymenea courbaril_ and _H. parvifolia_ trees in three of the home ranges flowered, all three agoutis began spending time near the tree, where they had not been before. Both

Hymenea species usually drop the previous season's fruits at the same time that it flowers (Miller 1991), but during the study period only one of the trees dropped a few fruits.

Although the agoutis fed on other items besides Pouteria while Pouteria was available, their movements depended on the location of the Pouteria trees. They fed heavily on Attalea pulp, but, with the exception of Female 163, did not have core areas in Attalea patches, perhaps because they do not hoard Attalea seeds.

Home Range Size and Densities

Home range size, calculated from both the foraging locations and the all day watch locations for each animal, ranged from 3 ha to 8.5 ha (Table 5-6). Due to the tracking methodology, which did not include all times nor the times of maximum patrolling activity, this is a minimum home range size estimate.

Observations of unmarked animals in areas in between monitored home ranges suggest that, at least in the immediate study area of the main trail system, agouti home ranges are closely packed together. Based on an average home range size of 5 ha, and assuming there are at least two adult agoutis per home range, the density of agoutis in the study site was estimated at 40 animals/km^2. This is at best a slight underestimate, because juvenile agoutis share territories with their parents.

Discussion

Food Availability and Use of Space

The use of space by agoutis in this study was similar to
that described by Smythe (1978), whose study was based on
trapping records and observations of animals near a baiting
station. Agoutis in both cases had core areas in their home
ranges (called "territories" by Smythe), and in both cases
these were determined by the location of productive trees.
When Pouteria seeds became scarce, agoutis on Maracá moved
away from their previous core areas. The results of both
studies indicate that agoutis respond to their habitat at the
individual tree scale, and that, despite their ability to
hoard seeds, they require several trees of different
preferred species within their home range to buffer both
seasonal and supra-annual variation in food supply.

At least two of the fruit species important in agouti
diets (Pouteria and Astrocaryum) alternated years of heavy
fruit production with seasons of low fruit production during
this study. Moskovits' (1998) 18 month fruiting phenology
study also shows that the height of peaks in fruit
availability can differ greatly between years, as different
species fail to fruit. Licania sp., which was heavily used
by agouti 163 in 1997, was also not available during the same
season the previous year. Rare trees, like Swartzia apetala

and Hymenea spp., which were not recorded as being heavily used during the study, are probably very important during certain years.

Spatial as well as temporal differences in fruit availability affected the foraging behavior and diet of individual agoutis in the tracking study. Female 163, whose home range was located in the low diversity, high Attalea density "Angico slope" forest type (Chapter 4), relied heavily on Attalea endocarps from October 1996 through at least January 1997. The fact that none of the other agoutis, in higher diversity habitats and with high Pouteria availability, used Attalea endocarps indicates that this palm is not a preferred food species. In a separate study of Attalea use by three mammalian species (Chapter 4), agoutis used endocarps only in the area adjacent to Female 163's home range, and in one other species-poor area bordering a Mauritia palm swamp. Both habitat types or plant associations were larger in extent than an agouti's home range, forcing animals established in that area to rely on non-preferred food items, at least during the study period.

An experimental study with white-winged trumpeters (Psophia leucoptera: Aves) in the Peruvian Amazon (Sherman and Eason 1998), showed that, for that fruit-eating species, the permanently defended territory size was determined at least in part by the need to provide sufficient food resources during the season of lowest fruit-availability, even if during the season of high availability resources

became superabundant. This should be true of any fruit and seed eating animal with a well-delimited and defended home range. In the case of agoutis, however, given their ability of to hoard seeds and to rely heavily on one tree species for several months, territory size must ensure an adequate food supply for supra-annual periods of food scarcity rather than seasonal periods. These would be times, for example, when palms and species in the Sapotaceae simultaneously fail to fruit. In both cases, the spatial distribution of trees and tree patches of different species in a habitat will have a strong effect on the home range size of fruit-eating animals. Because home range size influences other aspects of ecology and behavior, such as population density and the intensity of territory defense possible, the spatial distribution of trees can have an important impact on the structure of a community of fruit and seed eaters by determining the density and possibly competitive interactions among the members of the community.

Several species of fruit and seed eaters respond to fruit availability at the same individual tree scale as agoutis. Emmons (1980) describes use of "one to three localized areas" centered around fruiting trees for days at a time by African squirrels. Adler (1994) showed that spiny rats (Proechymis semispinosus) in Panama responded in a very localized way to fruit and seed availability. In his study, rat populations on small islands (1.7 to 3.5 ha, smaller than an agouti home range) showed among-island differences in

breeding season that corresponded to differences in the time when the dominant tree species on each island produced fruit. For small-bodied fruit and seed eaters, whose home ranges are smaller than the average extent of a plant association in the area they inhabit, differences among home ranges in the tree species available should alter demographic parameters among individual animals. One animal may breed earlier or have higher offspring survival than a neighboring animal, simply because of the identity of the trees that occur in its home range. Such a demographic response might tend to dampen population fluctuations in tropical forests, because mortality due to seasonal and minor supra-annual fluctuations in food availability would be spread out among individuals and among years. The extent to which this happens will be determined by the floristics of the area--species richness, number of rare vs. dominant species, and clumping tendencies of different species.

Home range size and population density

Home range size can affect population density by determining area used per individual or social unit. Other factors, such as predation, resource patchiness at the larger than home range scale (which would affect spacing between home ranges), food productivity levels, and competition with other species for food resources can affect population density. Comparisons of sites where population densities

have been estimated or calculated illustrate the difficulty of separating among these factors.

Home range sizes on Maracá were similar to or slightly larger than those reported by Hallwachs (1986; 4 ha) and Dubost (1988; 200 meter diameter area), but larger than those reported for Barro Colorado Island (BCI) by Smythe (1978; 1 - 2 ha). Agoutis were not radio-tracked in those studies, and methodology may have affected the range estimates. Additionally, on BCI home ranges were obtained for animals that used a baiting station; home ranges more distant from the bait site may have been much larger. It is also unclear whether Smythe includes all the area used by an animal in his territory estimates, or just the well-defended core areas. Some of Smythe's animals were juveniles, which may have smaller or less well-established ranges than adults; all animals in this study were adults. (This age difference may be a function of the capture methods, because dogs are likely to remain with an animal that goes into a shelter hole, and adults with established ranges are more likely to have reliable shelters than juveniles.) It is also possible, however, that the number of young animals is reduced by predation on Maracá relative to BCI, given the depleted predator population at BCI (Wright et al. 1994). To the extent that home range size is affected by population density, this would tend to both increase home range size and decrease apparent population densities on Maracá relative to BCI.

A comparison of densities reported from dry and humid forest in Central and South America shows surprising consistency and a few marked contrasts (Table 5-7). The lowest documented agouti densities are for the four sites in Peru. In the absence of information on home range sizes at these sites, it is difficult to determine the causes for density differences. As suggested by Janson and Emmons (1990), the low densities at Cocha Cashu, Peru, may be explained by periodic flooding of the study site; on Maracá, agouti sightings decreased markedly in riverine forest during the flood season, even though only a small portion of the transect itself was affected by flooding. This implies that either extreme shifting of habitat size or actual dispersal away from flooded areas occurs in these habitats, behaviors that have not yet been documented in tracking or capture-recapture studies. The remaining densities are within the same order of magnitude, from 27 animals per km^2 in Mexico (Coates-Estrada and Estrada 1986) to 64 in French Guiana (Dubost 1988). The most anomalous density is that of 63 agoutis per km^2 reported by Eisenberg et al. (1979) for a seasonal forest in northern Venezuela.

Several methodological biases may affect the reported densities, masking real ecological differences. Low densities at Bodmer's (unpublished data) sites in Peru may occur because animals are completely unaccustomed to humans other than hunters, and would tend to freeze at the approach of a human. At BCI, densities may be inflated relative to

other sites due to extreme habituation to humans (Wright et al. 1994).

The time of sampling, in relation to seasonality of fruit production, can also affect density estimates. On Maracá, there was a high frequency of feeding observations on _Pouteria_ and _Attalea_ for transects occurring when these preferred foods were in peak fruit fall, whereas there were no feeding observations on rarer food items. This suggests that at such times agoutis are very active around fruiting trees, making them more likely to be spotted. When food is more dispersed or less abundant, they are less conspicuous in their foraging behavior. This variation in behavior could affect density estimates obtained through transect sampling. Peres et al. (1997) do not cite the duration or season of their transect study, so it is impossible to judge the effect of either food availability or length of study on their data.

In French Guiana, agouti home ranges may not be as closely packed as on Maracá and BCI, due to the presence of acouchies; the density estimate based on home ranges may therefore be an overestimate. At Cocha Cashu, adding agouti and acouchy densities doubles the density of large, seed-eating diurnal rodents and brings it closer to other estimates. It may also be important to consider the effects of competitors such as white-lipped peccaries on agouti densities. The small home ranges on BCI and higher densities in hunted than unhunted areas in Peru (Chapter 4; Bodmer et al. 1997) suggest that competitive release may allow an

increase in agouti densities. In Peru, decreased primate populations may result in an increase in the availability of some species in the Sapotaceae to agoutis. On BCI, the absence of white-lipped peccaries would decrease some pressure on seed resources. Agouti densities on Maracá may currently be high due to a low white-lipped peccary population level; at times of high white-lipped peccary densities, anecdotal information points to a depletion of seeds and seedlings (J. Thompson, pers. comm.). During the current study, one agouti was noted to shift its core area after a white-lipped peccary herd passed through its home range and fed on <u>Pouteria</u> seeds in its core area. Both collared and white-lipped peccaries, as well as Echimyid and Murid rodents, feed on palm and Sapotaceae seeds, and their population densities should also be considered when examining competitive effects on agouti densities. This interaction with members of the terrestrial seed-eating guild may be as important as the presence or absence of predators in determining the population patterns of agoutis (c.f. Wright et al. 1994).

<u>Diet</u>

Agoutis on Maracá relied on a few plant species during the study period. This is similar to the situation on BCI (Smythe et al. 1996), where agoutis relied on the seeds of three plant species throughout the year, even though they

included a total of 36 species in their diet. On BCI, agoutis also fed heavily on non-preferred fruits such as _Tetragastris panamensis_ in years when those were abundant, indicating that important diet items may vary among years. Smythe (1978) also recorded agoutis feeding on fungi, and E. Naranjo (unpublished data) recorded frequent use of invertebrate animal matter. On Maracá, reliance on animal matter resulted from the use of beetle larvae in infested palm seeds (Chapter 4).

Sites that do not offer an array of a few abundant large-seeded items whose availability (phenology) is spaced throughout the year may not provide adequate habitat for agoutis, despite their ability to store seeds. This could be a partial explanation for low agouti densities at the Peruvian sites listed in Table 5-7. The high agouti densities in Peres et al.'s (1997) southeastern Brazil site may be due to the availability there of Brazil nuts (_Bertholletia excelsa_) in conjunction with _Attalea_ fruit and nuts. This extreme patchiness and availability of large-fruited species may be a characteristic of transitional forests (between moist forest and savanna), which occur at both the southeastern Brazil and the Maracá study sites, making such habitat particularly suitable for agoutis.

Seed Handling

The seedling clipping behavior exhibited by agoutis in this study is typical of many rodent species in a variety of habitats and biomes, and is probably a way of controlling seed degradation due to germination (Vander Wall 1990). Such behavior by agoutis supports the hypothesis that large size in Netropical seeds is an adaptation for surviving herbivory (Dalling et al. 1997, Harms and Dalling 1997, Mack 1998). But it may also be related to toxicity or ease of digestion of dead or older seeds. Collared peccaries were observed to scar _Pouteria_ seeds and then drop them, and to uproot _Pradosia_ seedlings and then return to feed on them a week later. Agoutis also uprooted _Pradosia_ seedlings that they did not eat, although they frequently ate freshly fallen or older, non-germinating seeds. Agoutis may thus manipulate seeds for reasons not directly related to food storage.

Table 5-1: Number of locations per animal.

Animal ID	Sex	Tracking Period	# of Loc.	All-day fol-lows	Fate
148	m	7-9-96 to 12-6-96	37	1	radio failed
158	f	7-9-96 to 11-30-96	38	2	killed
163	f	7-6-96 to 12-4-96; 2-10-97 to 3-31-97	41 20	2 3	sur-vived
167	f	7-3-96 to 11-23-96	37	1	killed
170	f	9-28-96 to 11-28-96	17	1	killed

Table 5-2: Eaten food items, with number of observations per item, from radio locations, transects, and casual observations.

Species	Family	Part	Radio loc.	Transects	Casual
Pouteria surumuensis	Sapotaceae	pulp	1	0	0
		seed*	37	20	
		seedling**	3		
Pradosia surinamensis		seed	22		1
		seedling	7		
Pouteria venosa		seedling	1		
Attalea maripa	Palmae	pulp	11	5	
		nut***	7		
Astrocaryum aculeatum		pulp	5		1
		imm. endosperm	2		
		nut***	3		
Mauritia flexuosa		fruit+		1	
Chrysobalanaceae sp.	Chrysobalanaceae	fruit+	3		
		pulp	4		
		seed	6		
Licania kunthiana		seed	1		
		seedling	9		
Hymenea sp.	Leguminosae	fruit+	1		
		seed	1		
		seedling	1		
		flower	1		
Inga sp.		imm. fruit	1		1
Tetragastris panamensis	Burseraceae	fruit+	1		

Table 5-2, continued.

Species	Family	Part	Radio loc.	Tran- sects	Ca- sual
		pulp	1		
Brosimum sp@	Moraceae	seed	2		
Eschweleira corrugata@		fruit+			
Passiflora sp.	Passiflor- aceae	fruit+	3		
Apeiba echinata	Tilliaceae	fruit+	1		
Apocynaceae sp.	Apocynaceae	seed- ling	1		
Cashew#	Anacardia- ceae	pulp (aril)			2
		seed			7
Mangifera indica#		seed			2
Apple#	Rosaceae	seed			1
Guava#		fruit+	1		
Unknown exotic pod		fruit+			1
Unknown seedling	Unknown	leaves	1		
Unknown seedling (2 sp.)		un- known	2		
Unknown fruit 1		pulp	1		
Unknown fruit 2		pulp	1		
Fungi					3
Pachymerus cardo	Bruchidae	larvae		1	2

* seed includes immature, ripe and old seeds
** seedling includes germinating seeds as well as seedlings with leaves
*** content not identified (larvae vs. endosperm)
+ could not distinguish if seed, pulp/aril, insect or several of these were eaten
# Cultivated or from trash
@ Noted only in 1997 when only one agouti was being tracked

Table 5-3: Number of <u>Attalea</u> <u>maripa</u> endocarps opened by
agoutis on Female 163's home range during the radio tracking
study.

Number of Endocarps Opened

Tree	Start Drop	9-7-96	10-15-96	11-15-96	2-12-97
D2	6-20-96	0	1	33	14
D1	7-10-96	0	73	87	146
D3	7-20-96	9	52	46	16
D4	8-15-96	2	8	13	22
AN2	9-1-96	0	0	6	204
Total Opened		11	134	185	402
Period Length			39 days	30 days	87 days
Endocarps /day			3.44	6.17	4.62

Table 5-4: Number of four focal tree species, gaps, and logs
in hole vs. core areas.

Species or Parameter	P-value	Core mean	Core s.d.	Hole mean	Hole s.d.
Attalea	0.44	2.21	1.76	2.21	3.17
Astroca-ryum	0.40	1.86	1.79	1.36	1.69
Pouteria	0.007	3.36	1.74	1.57	1.34
Pradosia	0.84	2.57	2.24	2.29	1.86
Small gap	0.4	1.14	0.86	0.93	1.07
Large gap	0.11	0.29	0.61	0.79	0.97
Log	0.98	0.5	0.23	0.43	0.17

Table 5-5: Trees of four key species found along the 2 km fruit availability transect, compared with the frequency with which agoutis were located in patches of the same four species.

|	*Attalea*	*Astroca-ryum*	*Pouteria*	*Pradosia*
Transect Trees	66	26	44	44
Radio Locations	44	29	63	43

Table 5-6. Home range size, day ranges, seasonal ranges, and number of locations used to calculate range sizes for the five agoutis tracked in this study.

Agouti ID (sex)	Time Period	Range Size (ha)	No. of locations
148 (m)	7-9-96 - 12-2-96	8.50	47
	7-9-96 - 9-15-96	7.69	22
	9-16-96 - 12-2-96	4.79	25
158 (f)	7-9-96 - 11-30-96	5.95	66
	7-9-96 - 9-15-96	3.36	19
	9-16-96 - 11-30-96	3.08	25
	12-hour range	2.27	24
163 (f)	7-6-96 - 3-31-97	2.94	123
	7-6-96 - 9-15-96	1.53	26
	9-16-96 - 12-4-96	2.21	25
	2-13-97 - 3-31-97	1.13	25
	12-hour range, 11-21-96	2.24	28
	12-hour range, 2-3-97	0.41	14
	12-hour range, 2-21-97	1.60	15
	12-hour range, 3-12-97	0.71	13
167 (f)	7-11-96 - 11-23-96	5.73	44
	7-11-96 - 9-15-96	3.97	22
	9-16-96 - 11-23-96	2.91	22
170 (f)	9-28-96 - 11-27-96	5.18	57
	9-28-96 - 10-31-96	1.92	10
	11-1-96 - 11-27-96	1.67	12
	12 hour range, 11-26-96	2.31	36

Table 5-7: Agouti density at forest sites.

Site	Density (ind/km^2)	Method	Reference
Peru: Samiria, unhunted, flooded	1.8	strip census	Bodmer, pers. comm.
Peru: Blanco, terra firme, hunted	2.3	strip census	Bodmer, pers. comm.
Peru: Terra firme, unhunted	1.8	strip census	Bodmer, pers. comm.
Maracá	40	radio tracked home ranges	Silvius, this study
Southeastern Amazonia	34	strip census	Peres et al 1997
BCI, old forest	58.5	strip census	Wright et al. 1994
Santa Rosa	38.8	observed home ranges	Hallawachs 1986 (in Wright et al. 1994)
Los Tuxtlas	27	strip census	Coates Estrada and Estrada 1986 (in Wright et al. 1994)
Sierra de Chamé	30	strip census	Hendrichs 1977 (in Wright et al. 1994)
Tikal	7.8	strip census	Cant 1977
Guatopo	63	trapping, strip census, road kill, correlations, other	Eisenberg et al. 1979 (in Wright et al. 1994)
Cocha Cashu, Peru	5.2	trapping, strip census, other	Janson and Emmons 1990
French Guiana	63.7*	observation of known animals	Calculated from Dubost 1988

* A "200 meter diameter" area = 3.14 ha per home range; this yields 31.2 home ranges per Km^2, and assuming two adult animals per home range, this yields adult density of 63.7 animals per Km^2.
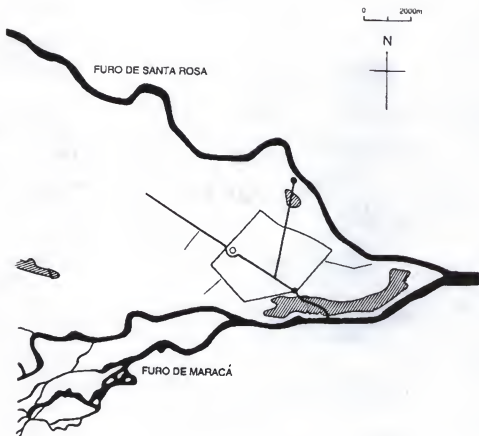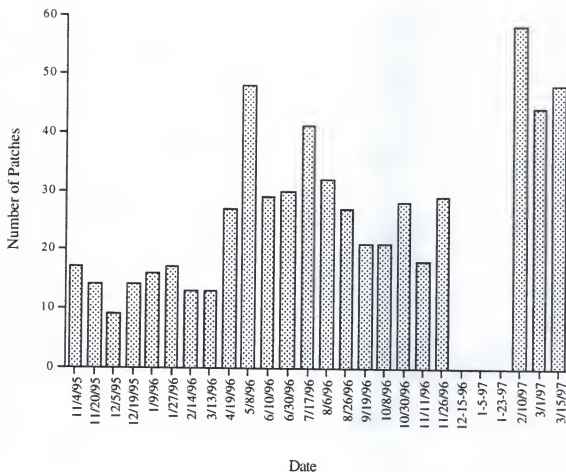
a)

Figure 5-1. Trail systems on the eastern end of Maracá
Island Ecological Reserve. a) Trails covered in mammal
transects; the center box includes a network of trails, shown
in part b; b) Close up of main trail system, with radio-
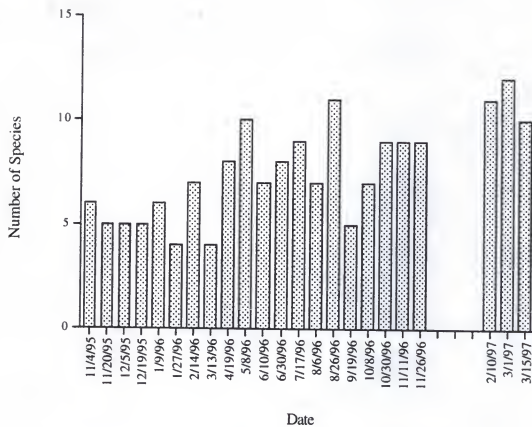tracked agouti home ranges.
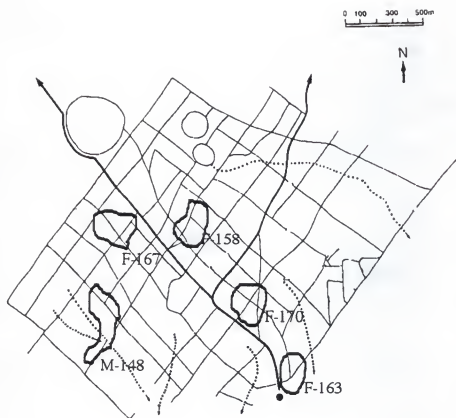
b)

Figure 5-1, continued.

a)

Figure 5-2. Availability, in terms of number of patches and number of plant species, found along a 2 km transect, of fruits and seeds considered edible for agoutis. a) Number of food patches; b) Number of edible species.
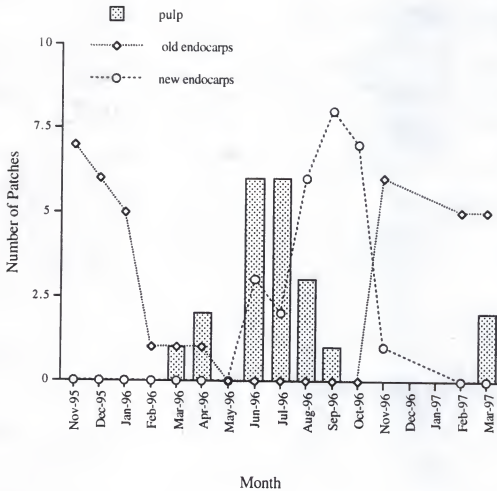
b)

Figure 5-2, continued.

Figure 5-3. Temporal pattern of availability of <u>Attalea</u> <u>maripa</u> pulp, new endocarps (from fruit dropped zero to six months previously, and old endocarps (from fruit dropped more than six months earlier).
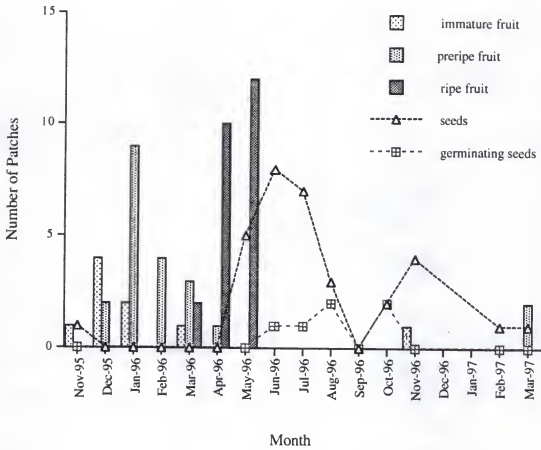
Figure 5-4. Temporal pattern of availability for <u>Pouteria surumuensis</u> fruits and seeds.
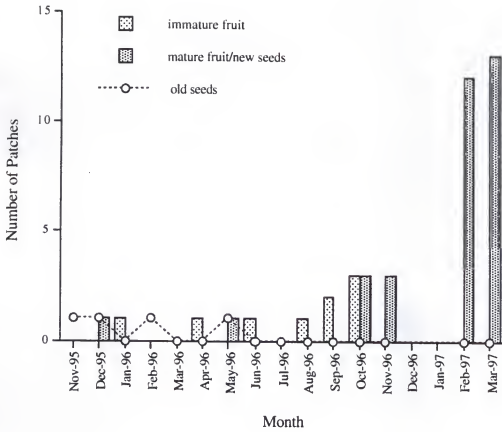
Figure 5-5. Temporal pattern of availability for <u>Astrocaryum</u> <u>aculeatum</u> fruits and seeds.
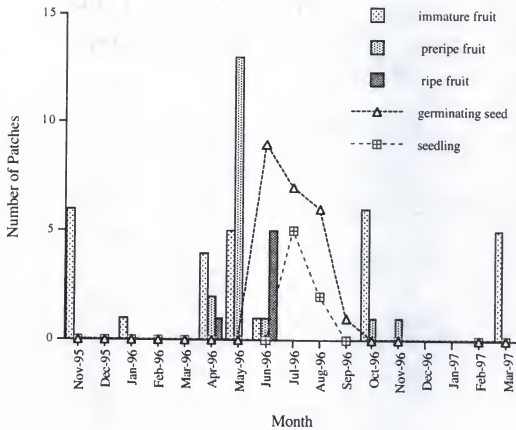
Figure 5-6. Temporal pattern of availability for <u>Pradosia</u> <u>surinamensis</u> fruits and seeds.
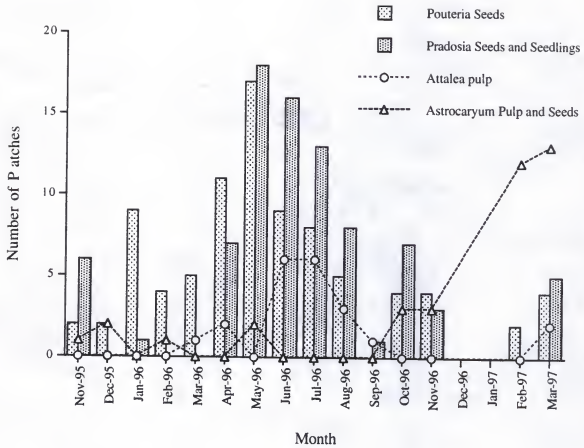
Figure 5-7. Congruent availability of the four principal food items for agoutis on Maracá (<u>Pouteria</u> <u>surumuensis</u> seeds, <u>Pradosia</u> <u>surinamensis</u> seeds and seedlings, <u>Attalea</u> <u>maripa</u> pulp, and <u>Astrocaryum</u> <u>aculeatum</u> pulp and seeds).

Figure 5-8. The seasonal range pattern for agouti 148 (does not include locations for 12 hr tracking period): ° = the July 9 to September 15, 1996 tracking period, and ▫ = the September 16 to December 2, 1996 tracking period. The different time periods correspond to periods of high and low <u>Pouteria surumuensis</u> seed availability, respectively.

Figure 5-9. The seasonal range pattern for agouti 158 (does not include locations for 12 hr tracking period): ° = the July 9 to September 15, 1996 tracking period, and ▫ = the September 16 to November 30, 1996, tracking period. The different time periods correspond to periods of high and low <u>Pouteria surumuensis</u> seed availability, respectively.

Figure 5-10. The seasonal range pattern for agouti 163 (not including locations for 12 hr tracking periods): ° = the July 6 to September 15, and ▫ = September 15 to December 4, 1996, and ▲ =February 13 to March 31, 1997.
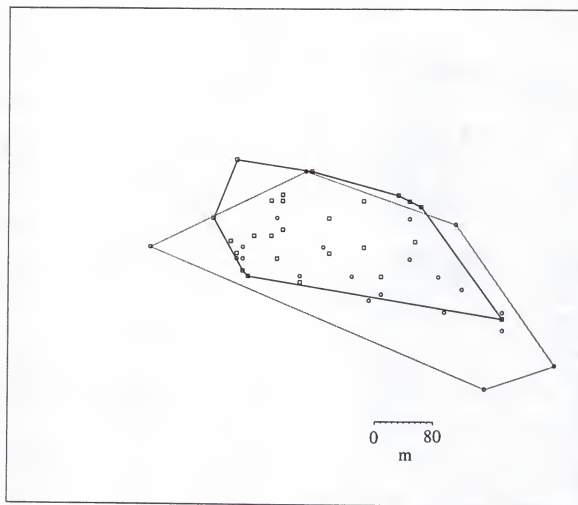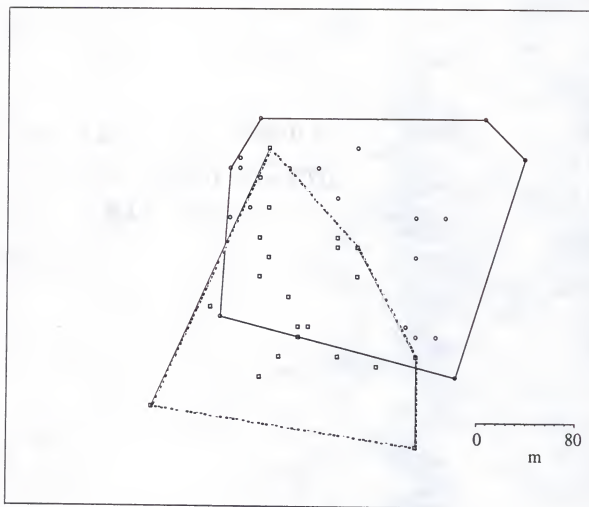
Figure 5-11. The seasonal range pattern for agouti 167 (does not include locations for 12 hr tracking period): ° = the July 11 to September 15, 1996 tracking period, and ° = the September 16 to November 23, 1996 tracking period. The different time periods correspond to periods of high and low _Pouteria surumuensis_ seed availability, respectively.
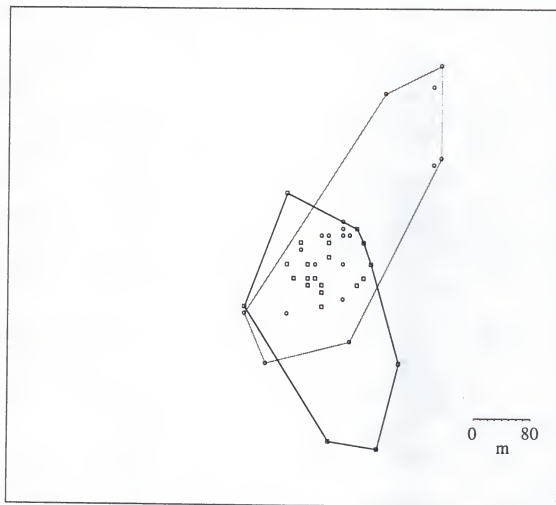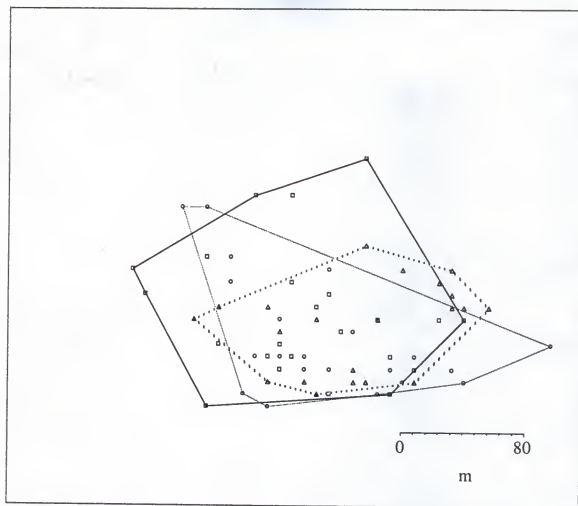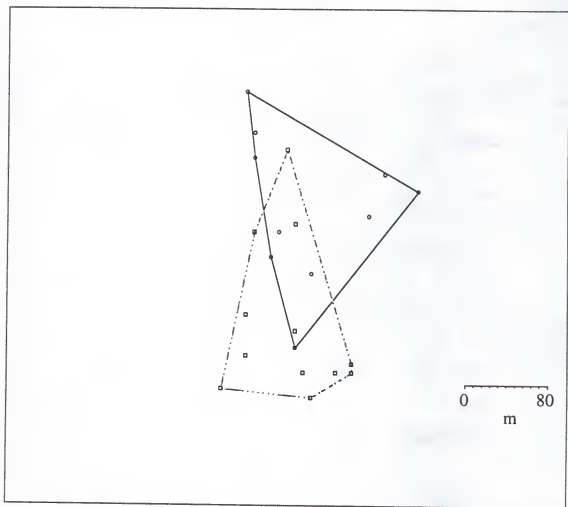
Figure 5-12. The seasonal range pattern for agouti 170 (not including locations for 12 hr tracking periods): ° = September 28 to October 31, 1996, and □ = November 1-27, 1996.
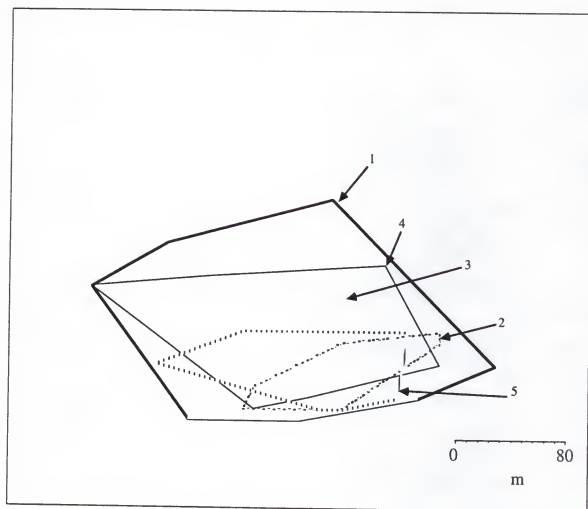
Figure 5-13. Four, 12 hr contiguous tracking range patterns for agouti 163, presented as subsets of the entire home range (1 in diagram): 2= 12 hr range on 21 November 1996, 3 = 3 February 1997, 4 = February 21 1997, and 5 = 12 March 1997.
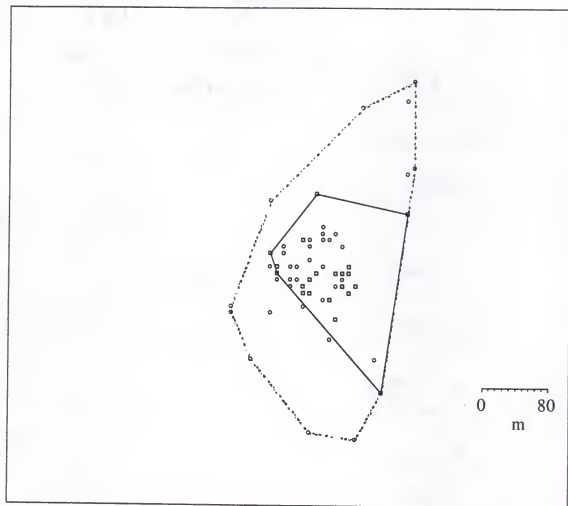
Figure 5-14. The 12 hr range pattern for agouti 158 (□)
presented as a subset of its total range (°;includes
locations for 12 hr tracking on 11-21-96)from July to
November 1996.
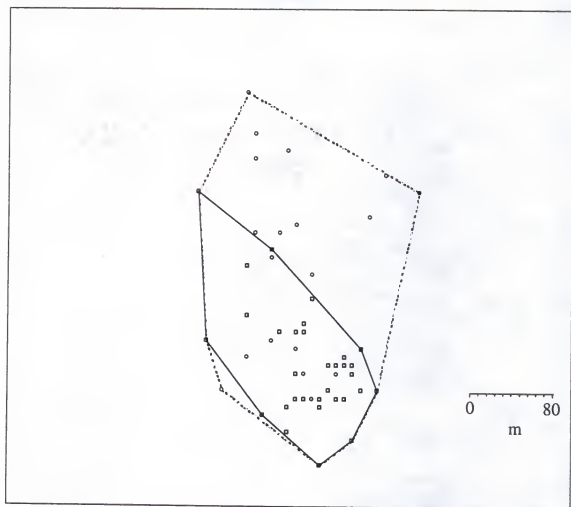
Figure 5-15. The 12 hr range pattern for agouti 170 (▫)
presented as a subset of its total range (○;includes
locations for 12 hr tracking on 11-21-96)from July to
November 1996.

CHAPTER 6
SCALE-DEPENDENT DISTRIBUTION PATTERNS IN PLANTS USED BY THREE
TERRESTRIAL RAIN FOREST MAMMALS AT MARACÁ ISLAND ECOLOGICAL
RESERVE

Introduction

Fruit- and seed-eating animals in tropical forests
encounter patchiness in food distribution at many scales.
Not only are fruits discretely distributed in space on
individual trees or shrubs (Chapman 1988, Fleming 1992),
individual tree species are also often distributed in a
clumped fashion within a few hectares or even a few meters
(Hubbell 1979, He 1993, Tuomisto et al. 1995, He et al. 1996,
Thorington et al. 1996). At the landscape scale (tens of
kilometers), species diversity, plant associations, or
habitat types can turn over rapidly within a few kilometers
(Milliken and Ratter 1989, 1998, Tuomisto et al. 1995, Foster
and Brokaw 1996, Chapman et al. 1997). Because distribution
patterns are a function of the scale at which they are
measured (Pielou 1977, Wiens 1995, Bellehumeur and Legendre
1998), different animal species with different home range
sizes and movement abilities will perceive different patterns
of distribution of the same resources at one site. As the
absolute scale or extent of the area used increases, the

grain size with which the animal measures it should also shift (c.f. Ims 1995, Kozakiewicz 1995).

Thus, an individual tapir (_Tapirus_ sp.) with a home range of several square kilometers, feeding on the ripe fruits of a species that is randomly distributed within one habitat type but patchily distributed among habitats, is able to move between fruit rich habitats. It perceives a high level of food availability at the time when the tree species in question is fruiting. A spiny rat (_Proechimys_ sp.) or squirrel (_Sciurus_ sp.) restricted to a home range of one hectare, on the other hand, may not encounter a single fruiting tree of this species and experience a time of food shortage at the same time that the tapir--or even a neighboring spiny rat (c.f. Foster and Brokaw 1996)-is finding adequate food. The small scale to which individual rats are restricted may lead to source sink dynamics at the rat population level, whereas similar dynamics may not occur for the more mobile tapir.

Scale dependency of food availability holds true for all animals in all biomes. The situation is particularly interesting for studies of tropical fruit-eaters, however, because in tropical forests patchiness involves a much higher diversity of tree species and functional groups, and is prevalent at all scales (e.g. Tuomisto et al. 1995, Thorington et al. 1996). In studies where resource distribution is an important variable, such as in correlations between foraging behavior, social structure, or

interspecific competition and resource distribution, it is therefore critical that resource distribution be measured at the same scale at which the animal or population under study perceives it. This is seldom done, because a) the scale and grain size at which the animals sample the environment is not known prior to the study; b) in community level studies, it is too cumbersome to measure resource distribution at a different scale for each species; and c) it is labor intensive to quantify tree distribution in high diversity tropical forests. In studies of sympatric primate species (Terborgh 1983), for example, or even sympatric frugivorous species in different orders (Chapman et al. 1989), the same plots or fruit trap layouts have been used to measure resource availability and indices of tree dispersion for several species with different home range sizes, territoriality, and movement abilities.

As long-term studies at single sites become more common, and information accumulates on several locally sympatric species or on individuals with overlapping territories, an examination of resource use at different scales and its implication for ecological interactions becomes feasible. In this paper I take advantage of the existence of forest inventories and mammal tracking studies over the last two decades at Maracá Island Ecological Reserve, in the northern Brazilian Amazon, to describe animals that use the same resources but have very different home range sizes and may perceive food availability differently in their environment.

I use the known home ranges and foraging distances of three species of Neotropical terrestrial fruit eaters studied at one site as "meter-sticks" with which to measure patchiness in their environment. The home ranges of white-lipped peccaries (<u>Tayassu</u> <u>pecari</u>-20-200 km^2) collared peccaries (<u>Tayassu</u> <u>tajacu</u>-10 km^2), and agoutis (<u>Dasyprocta</u> <u>agouti</u>-0.05 km^2) differ by several orders of magnitude. I summarize the overall species diversity differences among terra firme habitat types, and then focus on terra firme canopy and sub-canopy tree species that are important in the diet of all three animals at this site. I predict that each animal species will encounter a different distribution pattern of the same tree species, and that the animal species' ranging behavior will in part reflect this perception of resource distribution. Although I focus on the individual animal's or herd's perception of spatial variation the environment, I speculate on potential differences at the population level.

Study Site

Maracá Island Ecological Reserve is a 1,100 km^2 riverine island located on the forest side of the forest-savanna boundary that marks the transition from the Rupununi savannas of Guyana to the Amazonian rain forest in the northern Brazilian state of Roraima. Floristic, geomorphological, and faunal inventories were described on the reserve during

an intensive multidisciplinary survey by the Royal Geographic Society and the Brazilian National Institute for Amazonian Research (INPA) in 1987-88. The entire reserve, which lies parallel to the transition gradient, grades from small savannas, transitional forests and high diversity moist upland forest in the east, through an area dominated by the deciduous legume _Peltogyne gracilipes_ in the center and center east, and moist upland mixed forests in the west. There is ongoing discussion as to the degree to which forests on the eastern end of the reserve, where most studies have taken place, have undergone human disturbance (Proctor and Miller 1998). Disturbance probably involved clearing of small patches of forest; no forest clearing has taken place during the last 110 years.

Maracá is located on the Guiana Complex portion of the Guiana Shield, and includes the transition between a Plio-Pleistocene substrate at the eastern side and a late Tertiary formation on the western portion (Thompson et al. 1992). The eastern terrain is flat and low, while the western terrain is higher and more dissected by hills and ridges. Elevation ranges from 110-160 meters above sea level on the eastern half of the island, and from 330-350 meters above sea level on the western portion of the island. The soils are sandy and derived from quartz-biotite schists, quartz-feldspar gneisses, and tonalitic granites (Thompson et al. 1992).

Rainfall records on the eastern end of the island show variation between 1750 and 2,300 mm annually (Thompson et al.

1992); during El Niño Southern Oscillation events, rainfall decreases markedly across the state (unpublished data, Brazilian airforce records). The wet season is between May and September, the dry season between October and April, with rains starting in either early or late April. The heaviest individual rains tend to fall in the dry season (Thompson et al. 1992, Milliken and Ratter 1998).

Floristics

The plant families with the greatest number of tree species on terra firme habitats are the Leguminoseae, Rubiaceae, Moraceae, and Burseraceae (Milliken and Ratter 1989, 1998; all vegetation descriptions are from these sources). Based on importance value (IV = relative density + relative dominance + relative frequency) rather than species richness, Sapotaceae is the dominant family in the eastern forests (always within the top 5 families in each transect). Rubiaceae, Moraceae, Burseraceae, Annonaceae, Chrysobalanaceae, Palmae and Bignonaceae also occur within the top 5 dominant families based on IV in transects on the eastern end. Sixteen species of palm and 16 of Sapotaceae occur on the island, with <u>Attalea maripa</u> and <u>Astrocaryum aculeatum</u> the most common terra firme palms, and <u>Pradosia surinamensis</u>, <u>Pouteria surumuensis</u>, <u>P. venosa</u>, and <u>Ecclinusa guianensis</u> the most common species in the Sapotaceae.

There is a gradual increase in diversity and turnover of species from east to west on the island. Only 26% and 40% of the tree species encountered on the eastern and central terra firme forests respectively were also encountered 60 km away on the western-most areas sampled. Family composition also changes from east to west: the Sapotaceae, so important in the east, contributes little to IV on the west. In contrast, the Euphorbiaceae becomes common on the west, though it was very poorly represented in the east. None of the top five families and only four out of the top ten families are common to the eastern- and westernmost transects (Milliken and Ratter 1989, 1998).

There are no extensive flooded forest habitats or palm swamps on the Reserve, although the riverine forest floods in low pockets during high rainfall years (Milliken and Ratter 1989, Fragoso 1994). Several small ponds and savannas are interspersed throughout the forest, and frequent strands of _Mauritia flexuosa_ palms run along stream courses and other periodically flooded habitats.

Study Animals

White-lipped peccaries and collared peccaries were tracked by Fragoso (1994, 1998, in review, unpublished data) during two study seasons. A herd of 40 white-lipped peccaries tracked for 12 months in 1991-9 had a home range of 21 km^2, while a herd of 130 animals tracked for six months

had a home range of 109 km^2. Two herds of collared peccaries tracked for six months (21 individuals) and eight months (36 individuals) had home ranges of 11 and 10 km^2 respectively. In 1995-97, a herd of 70 white-lipped peccaries tracked for 17 months, and a herd of 200 tracked for 19 months had home ranges of approximately 50 and 150 km^2. During the same time period, three herds of collared peccaries with between 20 and 30 individuals had home ranges of approximately 10 - 15 km^2 (Fragoso unpublished data). Herds were usually located aerially twice a week. Casual encounters with the animals on the trail system increased the sample size for locations there. Agoutis were radio tracked as part of this study to determine the scale at which they used their habitat (Chapter 5). Home range size for six radio collared animals tracked for between 2 and 8 months was 0.03 to 0.08 km^2 (Chapter 5).

Both collared peccaries and agoutis are territorial, engaging in agonistic behavior to defend home ranges against conspecifics (Fragoso 1998). White-lipped peccaries, on the other hand, do not defend their large home ranges, and in this study the ranges of the two known groups overlapped extensively (in space but less frequently in time). They also overlapped with the home ranges of all three collared peccary herds. Unlike both peccary species, agoutis patrol most of their home range at least once a day. However, each day they concentrate foraging (including feeding and burying seeds) at only a few individual trees (Smythe 1978, Chapter 5). Collared peccaries tend to feed at one or a few patches

of trees, or at one very large tree, such as an _Enterolobium_, during one day. White-lipped peccaries will forage over several kilometers of forest in one day, and frequently move between habitat types in a single day. For this study, the scale at which the animals operate is set at their home range size (known a priori), and the grain size at which they measure the environment is assumed to be equivalent to the food patch size (one tree for agoutis, one group of trees or patch for collared peccaries, one habitat type for white-lipped peccaries; Table 6-1).

Both species of peccaries and the agoutis on the trail system relied heavily on the palm _Attalea maripa_, and the sapotaceous species _Pradosia surinamensis_ and _Pouteria surumuensis_ (Chapter 4, Fragoso 1994). Other large fruited tree species known or suspected to be used by the three species are included in this study: all species in the Lecythidaceae and Sapotaceae, the palm _Astrocaryum aculeatum_, _Couepia_ sp. and _Licania kunthiana_ (Chrysobalanaceae), _Enterolobium_ spp. and _Hymenea_ spp. (Leguminosae), and one unidentified species in the Icaniaceae (Appendix 1). The only small-fruited plant species used by all three animals was _Brosimum lactescens_ (Moraceae).

Methods

Data Collation from Previous Studies

The home ranges of white-lipped peccary herds radio
tracked by Fragoso in 1991-93 and 1995-97, and collared
peccary herds tracked in 1995-97 were plotted on a map of the
study site. The location of all forests plots inventoried on
Maracá by Milliken and Ratter (1989) and Nascimento (1994) in
terra firme forest (upland) habitats were plotted on the same
maps. Only terra firme habitats were considered, to avoid
the distinct patchiness and moisture-adapted species
associations created by poor drainage conditions in lowland
and flooded areas. For each forest inventory plot, I noted
the dominant species (more abundant by at least 10
individuals than the next most common species) and noted the
number of trees of each species known to be important in the
diets of agoutis and peccaries. Information on the habitat
type, area sampled, overall tree density, and diversity are
also given for each plot when available. In most cases trees
were sampled at both the 30 and 10 cm dbh categories; I chose
to use the 10 cm dbh category in order not to under-sample
the abundance of _Pouteria surumuensis_, (individuals with less
than 30 cm dbh bear fruit and are common) and of several
arborescent palms that never attain 30 cm dbh. Additionally,
equivalent plot size for 10-cm dbh in Milliken and Ratter
(1989), who used a point center quadrat method, was most

similar to the 0.25 hectare plot size used by Nascimento
(1994). A visual comparison with data for 30 cm dbh plots
showed no obvious differences in abundance for any of the
species being considered.

Fruit and Seed Availability on the Ground in Three Habitats

Because I was working with terrestrial consumers, fruit
and seed availability was monitored on the ground rather than
on the tree. Three two-kilometer long transects were marked
along two existing and one newly cut trails in three terra
firme forest types (riverine ("river trail"), eastern ("trail
2"), and central ("km 7")) known to be used by a single herd
of white-lipped peccaries and to be floristically distinct
based on Milliken and Ratter (1989) (Chapter 4). The two
terra firme transects were separated from each other by 6
kilometers, and from the riverine forest by 3 and 9
kilometers respectively.

Each transect was marked at 50 m intervals, yielding
forty 3 x 50 m quadrats or segments per transect. Every two
to three weeks (mean sampling interval 20.76 days, range 30 -
14 days) from November 4 1995 to October 13 1996, the ground
along a 3 m width was surveyed for fruits and seeds.
Sampling started two weeks later in the central terra firme
forest, and two scheduled samples were missed. The location
(segment number) of each fruit patch was noted. Species were
identified using on-site reference collections and van

Roosmalen (1985). Fruit items were not collected, and were recounted on subsequent transects if they were still in edible condition. While ground surveys do not give an estimate of the quantity of food available on the ground, because of rapid fruit removal by consumers, they do capture the same spatio-temporal patterns of fruit production as arboreal surveys (Zhang and Wang 1995, Stevenson et al. 1998). In addition, ground transects document post-dispersal availability (older seeds and seedlings; Chapter 5).

In this study a species was considered available through all of its edible stages, not just when it was ripe. For example, in the case of _Pradosia surinamensis_, unripe seeds are eaten by collared and white-lipped peccaries, unripe and ripe seeds are eaten by agoutis, and germinating seeds are eaten by all, while _Attalea_ endocarps remain edible for up to a year after fruit fall (Chapter 4, 5). All fruits, seeds, and germinating seeds encountered were recorded. Seed patches produced by animal defecations were also counted; in the case of spider monkey sleeping trees and tapir latrines (Fragoso 1997), accumulated defecations resulted in large patches of seeds in the same location over several transect runs.

For each transect, adult trees of _Attalea maripa_ were counted in each segment, within 2.5 m of the center of the trail, yielding forty 5 x 50 m plots per transect. Additionally, _Pouteria surumuensis_ trees were counted along the transect in eastern terra firme forest.

The three transects are compared in terms of fruit species diversity, number of fruit patches available per segment and per transect over one year, differences in timing of peak fruit availability, and contribution of the "edible" species to overall patterns of availability. At the smallest scale, the index of dispersion of edible food patches was calculated for aggregated quadrat sizes from 50 m long to 1000 m long, and the clumping pattern compared among transects. Distribution indices based on an aggregation of quadrats cannot be tested for statistical significance, due to lack of independence of adjacent and summed quadrats (Pielou 1977). However, patterns shown by variance peaks at aggregate quadrate sizes less than half the length of the total quadrat are generally accepted as indicative of real pattern free from sample size influence (Ludwig and Reynolds 1988, Campbell 1998). No index of dispersion can be calculated for the floristic plots from Milliken and Ratter (1989) and Nascimento (1994), because data were gathered using different methodologies and on plots of different sizes.

<u>Results</u>

<u>Floristic Plots</u>

<u>All species</u>

The 30 terra firme forest quadrats sampled in the floristic plots ranged in area from 0.06 to 0.5 ha (Appendix 2). They were concentrated on the central trail of the main trail system, in a <u>Peltogyne</u> rich area to the southeast, and on two trails in the center west and west (Figs. 6-2 and 6-3). No plots have been established in riverine forest on Maracá. Number of trees sampled ranged from 40 to 200, and number of species per plot from 15 to 54 (Appendix 2). For purposes of comparison between general areas on the Reserve I have grouped the plots into eastern trail system (plots 1-11), center east/<u>Peltogyne</u> (plots 12-24), center west (plots 25-29) and west end (plots 29 and 30) (Figs. 6-2, 6-3). Twenty one out of the 30 plots showed clear dominance by at least one and usually several equally abundant species (species more abundant by at least 10 trees than the next most abundant species), and five more showed a trend for one species to dominate. Information on dominance in terms of numbers of individuals is used here to show turnover across the landscape of these species; abundant species are more reliably tracked than rare ones. The three smallest plots showed no species dominance, suggesting an area effect. Six

species dominated in more than one plot: <u>Peltogyne</u> (6 plots), <u>Pradosia</u> (5 plots), <u>Tetragastris</u> (3 plots), <u>Licania</u> (3 plots), <u>Ecclinusa</u> (6 plots) and <u>Attalea</u> (2 plots); while three species were dominant in one plot each: <u>Himatanthus</u>, <u>Oenocarpus</u>, and <u>Alseis</u>. Frequency of dominance does not reflect frequency in the Reserve, because plots were not placed at random.

<u>Edible species</u>

<u>Sapotaceae trends</u>. <u>Pradosia</u> was common everywhere on the eastern areas (Table 6-2). Despite its ubiquitous presence, pattern at the scale of hundreds of meters is revealed by the plots: plots 3,4, and 5 have almost no <u>Pradosia</u>, whereas this species is dominant in plots 1 and 2, located about 300 meters away. This concurs with my observation that <u>Pradosia</u> occurs in frequent long swaths through the forest, interrupted by <u>Pradosia</u>-free areas. <u>Pradosia</u> and <u>Ecclinusa</u> are the only sapotaceous species that remain common in the central/eastern <u>Peltogyne</u> forests, before disappearing in the west. <u>Ecclinusa</u> is most common in the center east, and also exhibits small scale patchiness: plots 15, 16, and 17 are adjacent to each other, but only 17 has a high abundance of <u>Ecclinusa</u>. <u>Pouteria</u> <u>surumuensis</u> appears to have the widest range of any of the Sapotaceae, occurring in the center west before dropping out in the west. It is associated with <u>Pradosia</u> everywhere but in the <u>Peltogyne</u> forest. The same is

true of _P_. _hispida_ and possibly _P_. _venosa_, though sample sizes are small for the latter species.

Palm trends. _Oenocarpus_ _bacaba_, rare and patchy in the east, becomes relatively more common in the center east and west. Only three _O_. _bacaba_ patches have been found on the eastern trail system (Fragoso unpublished data), and all are characterized by high local density and discrete boundaries. The sites differ in topography (one is a flat upland area, one is on a slope, and one on a bottomland). _Attalea_ _maripa_ is common in the east, but becomes less common in the center east, more easterly than any of the Sapotaceae. _Attalea_ patches appear to be larger but more infrequent than _Pradosia_ patches, since adjacent plots tend to have similar numbers of this palm (Table 6-2). _Attalea_ does not co-occur with _Peltogyne_. _Astrocaryum_ _aculeatum_ appears to be less aggregated, or to be aggregated at lower densities than _Attalea_ _maripa_. Like _Attalea_ _maripa_, it does not co-occur with _Peltogyne_, and it drops out even sooner (more easterly). In general, palms are much less common in the western half of the island; _Jessenia_ (_Oenocarpus_) _bataua_ replaces the eastern species, but never becomes as abundant in individual plots as _Attalea_ or _Astrocaryum_.

Other edible species trends. _Tetragastris_ and _Licania_, important to primates as well as agoutis and peccaries, are common and apparently clumped in the east, but absent in the

west and in _Peltogyne_ forest (Table 6-2). Two species of
Enterolobium and _Hymenea_ are rare everywhere, but more common
in the east than west. In the Lecythidaceae, distinct
understory species are common in the east and west
respectively, with only _Gustavia superba_ occurring in both
areas. _Lecythis corrugata_, common in all eastern plots, drops
out in _Peltogyne_ and in the west. It co-occurs with both
palms and sapotaceaous species, and does not appear to be
patchy to the same degree the other species considered here
are, based on similar abundances in all plots and absence
from none.

The above descriptions refer to interior terra firme
forests. Floristic plots have never been established in
riverine forest on Maracá. Milliken and Ratter (1989, 1998)
describe the composition of riverine forest on Maracá as
follows. On the eastern half of the island, to the second
Santa Rosa hump (Fig. 6-2), the most common species are
Attalea maripa, _Chochlospermum orinocence_, and _Spondias
mombim_. Of these, only _Attalea_ is common in terra firme
forest as well, based on my transect results. _Spondias_
occurs only in two small patches on the main trail system
(pers. obs.). The large emergents _Enterolobium_ spp., _Ceiba
pentandra_ and _Andira inermis_ are also more common on the
river than on terra firme, though they are still widely
spaced. In low, flooded areas of the river bank, _Triplaris_
is a colonist. On the western river edges, which are much
steeper than the eastern ones, the terra firme forest tends

to extend down to the river bank. Contrary to what occurs in
the central terra firme forest, _Attalea_ remains common in
Peltogyne forest when this forest type reaches the river
bank.

Peccary Ranges Overlain on Floristics

The two white-lipped peccary herds tracked in 1995-97
and the larger herd tracked for six months in 1992 would have
encountered the full floristic variability of the eastern and
center eastern areas, including the riverine forest (Fig. 6-
3). Any white-lipped peccary herds that used the areas to
the west would have encountered very different floristics,
and may have had diets lower in fruit than the eastern
animals (no herds other than the radio-tracked herds ever
visited the main trail system, though untracked herds may
have overlapped with the study herds in the center east;
pers. obs.). The largest white-lip herd was never radio
located within the central _Peltogyne_ forest, even though it
did use use _Peltogyne_ forests on the south east--the area
where _Pradosia_ is most common (plots 20-23).

During the transect study, I encountered white-lips 7
times. Twice when white-lips where encountered on the river
forest they were feeding on _Attalea_ endocarp contents and
Phenakospermum stems. At least one herd repeatedly visited
the river forest near the station during the 1995-96 and
1996-97 dry seasons, the time when _Attalea_ endocarps are

available (Chapter 3). Two times when white-lips were encountered foraging rather than traveling on the main trail system they were feeding on <u>Pouteria surumuensis</u>, once on <u>Pradosia</u>, and once on <u>Enterolobium</u>. In the center east, they were encountered foraging in a <u>Mauritia</u> palm strand, feeding on the seeds of three palm species (<u>Euterpe precatoria</u>, <u>Socratea exorrhiza</u>, and <u>Mauritia flexuosa</u>), and once feeding on <u>Attalea</u> endocarps and <u>Hymenea</u> seeds. With the exception of <u>Phenakospermum</u> stems, all these food items had been previously recorded by Fragoso (1994, 1998), pointing to a high temporal consistency in the diets of white-lipped peccaries in the study area.

The collared peccary herds tracked in 1995-97 all partitioned the eastern tip of the island in such a way that each herd had a portion of the Sapotaceae-rich terra firme forest, and a portion of the palm and <u>Spondias</u>-rich riverine forest. The white-lipped herd tracked in 1992 (Fig. 6-3b) saw a similar habitat diversity, but it used all the terra fime area and the river banks on both sides of the island. It avoided the treeless savanna/wetlands on the very eastern part of the island, although it used a small savanna/wetland on the southern border to feed on fish. None of the collared peccary herds included savannas in their home range.

Fruit Transects

Overall fruit availability

Over an 11 month monitoring period, I sampled the River Trail and Trail 2 (eastern terra firme forest) 18 times, and the Km 7 Trail (central terra firme) 15 times. Km 7 had the highest total fruit species diversity, but the lowest number of fruit patches and highest number of empty segments per sample (Table 6-3, and Fig. 6-4a-d). The River Trail, despite its low species diversity, had the highest number of patches per transect. This was due in large part to the high density of _Attalea_ _maripa_ palms, which was the dominant species in 12 out of 18 transects and contributed to the higher number of patches per species on the River Trail compared to the other two transects. _Attalea_ dominated only in 5 transects on Trail 2 and Km 7, whereas sapotaceous species dominated in 9/18 and 8/15 transects in Trail 2 and Km 7 respectively. No Sapotaceae occurred on the River Trail (a small clump of _Pradosia_ trees produced no fruit during the study). No other families or species overtook Sapotaceae and _Attalea_ in frequency of dominance.

All trails showed a short peak in total fruit availability in January 1996 (the mid dry season; repeated in January 1997 for Trail 2; Chapter 3) and a broader peak in May - August (the early and mid rainy season).

Edible fruit availability

All species known or expected to be eaten by peccaries
and agoutis were grouped as "edible species" and analyzed
separately from the remaining fruits (Appendix 1). The River
Trail had 7 edible species, while Trail 2 and Km 7 had 15 and
17 edible species respectively. When the contribution to the
temporal pattern of fruit and seed availability of palms,
Sapotaceae, other edible species and all edible species is
plotted against the total fruit pattern for each trail (Fig.
6-5a-c) the following patterns emerge: On the River Trail,
temporal pattern in edible species availability closely
follows total species availability, and the pattern is set by
Attalea maripa (Fig. 6-5a). On Trail 2, edible species make
up a smaller proportion of total availability and peak at
different times; the pattern of edible species availability
is set by the Sapotaceae (Fig. 6-5b). Furthermore, palm
fruit and seed availability peaks when Sapotaceae
availability is low, and vice versa. The same is true on Km 7
(Fig. 6-5c). Because the river trail is palm driven and the
other two trails Sapotaceae driven, and because the time of
avaialbility of the two classes of items are displaced from
each other, food is available on the River Trail at the time
when it is scarce on the terra firme forest, and vice versa.
White-lipped peccaries and collared peccaries including both
habitats in their home ranges would be able to use both peaks

(but note that this is more true for white-lips, which can
use the _Attalea_ seeds, than for collared peccaries, which
only use the pulp; Chapters 3, 4).

Agouti scale: within-habitat patterns of edible species availability

To examine aggregation in space rather than time within
each habitat, for each segment of each trail I extracted the
number of patches of each edible species that occurred in the
transect sample with the maximum number of patches for that
species during the study period, and summed across all edible
species. This estimates (slight underestimate, if trees of
the same species were not in synchrony) the number of trees
in each segment that produced edible fruit during that
seasonal cycle. Trail 2 showed a pattern of peaks at 50 to
100 meter intervals, overlain by a larger-scale bimodal
pattern at 100 meters (Fig. 6-6a). This pattern was again
driven by the location of palm and Sapotaceae patches, with
the additional contribution of several _Couepia_ sp. and
Eschweleira _corrugata_ trees at 300 - 500 meters along the
transect. Km 7 also shows a pattern of peaks at 50 - 100
meter intervals, with an overlain pattern at 500- 600 m
intervals (Fig. 6-6b). The pattern is driven almost
exclusively by Sapotaceae. The River Trail pattern differs
from the other trails in having more closely spaced peaks
with greater variation in the spacing between peaks (Fig. 6-

6c). The pattern is driven by <u>Attalea</u> with some contribution from <u>Spondias mombin</u> at 1200-1300 meters.

These results are summarized by the trend in indices of dispersion calculated at different aggregated plot sizes (Fig. 6-7). An index of 1 reflects an even or dispersed distribution, an index of less than 1 reflects a random distribution, while and index greater than 1 reflects an aggregated distribution (Krebs 1989). I cannot test the deviation from 1 statistically because I aggregated plot data and the samples are therefore not independent. The River Trail shows the pattern typical of a random distribution, with slightly fluctuating variance-to-mean ratios (Ludwig 1988). Trail 2 and Km 7 both show peaks in variance-to-mean ratios at 300 to 400 meters, indicating that there are 150-200 meter segments of the trail with high fruit availability interspersed by similar length segments with low fruit availability. In other words, the habitat is patchy at the scale of 150 to 200 meters. The similarity between the two habitats is probably due to the dominance of Sapotaceae in both. The bimodal pattern detected for Trail 2 is revealed by the near 0 ratio at the 1000 m interval, whereas the ratio remains similar to that of other plot sizes for the River Trail and near peak for Km 7.

Agouti home ranges averaged just over 0.05 km^2 in size. Core areas were located within 150 by 150 meter areas (Chapter 5). Thus at the scale of activity of individual agoutis, the terra firme forests are patchy due to species

aggregations (palm and Sapotaceae driven pattern). The riverine habitat, on the other hand, has a random pattern of availability at a scale smaller than what the agoutis use, and a random or self-similar availability at larger scales (within the 2 km sampled). Individual agoutis living in the two habitat types thus encounter different patterns of availability, although they are separated by only a few kilometers.

Discussion

Species-Specific Perspectives

Focusing on the tree species actually used by the study animals rather than on community wide-patterns of availability helps elucidate and simplify spatio-temporal patterns of food availability. At the landscape scale, the food species monitored in this study followed the overall east to west species turnover noted by Milliken and Ratter (1989, 1998). Although many of the species still occur on the western end of the island, and even in the foothills of the Parima mountains, there they become very rare, in contrast to their dominance and extensive patch size in the east.

White-lipped peccary scale

When the trend in vegetation turnover across the
landscape is truncated at the white-lipped peccary home range
scale, some species become a constant while others remain
patchy. Thus Pradosia surinamensis and Pouteria surumuensis
are found in all the terra firme forest visited by white
lipped peccaries, while Attalea maripa is concentrated on the
easternmost portion and becomes rare in the center east. The
small scale patchiness in palm and Sapotaceae distributions
detected with the index of dispersion occurs at too small a
scale to be noted by animals like white-lips, which operate
at a large grain size and move one or two kilometers along a
single patch of food.

The fact that in both 1995 and 1996, white-lipped
peccaries started visiting the river trail during the same
month (October) to feed on Attalea endocarps, and continued
to visit it until the late dry season in February, suggests
that individual white-lip herds make foraging decisions at
the habitat mosaic scale (habitats clearly distinguishable to
the human eye based on edaphic as well as floristic
variables). The riverine forest is a seasonally food rich
habitat; Attalea endocarp contents are maximally available
between September and April (Chapter 4).

White-lipped peccaries use other seasonal habitats
(Mauritia wetlands, ponds, and savannas, which flood for
various amounts of time) more than expected based on their

availability in the environment, and terra firme forests less than expected (Fragoso 1994, in press). This suggests they use terra fime forest as one more habitat patch, to be visited when food, primarily Sapotaceae fruits and seeds, are available there. The <u>Mauritia</u> wetlands they rely on are seasonal with respect to the availability of fish and invertebrates (high at the end of the wet season) but aseasonal with respect to the availability of fruits. <u>Mauritia</u> is an irregular aseasonal fruiter; within one wetland trees fruit synchronously, but among wetlands they do not (Moskovits 1985, Fragoso unpublished data, Silvius unpublished data). From the point of view of animals that can visit several wetlands in one foraging bout, they provide food continuously.

Collared peccary scale

On Maracá, collared peccaries seldom use seasonal habitats such as riverine forest, <u>Mauritia</u> wetlands and savannas (Fragoso 1994, in press). They are confined mostly to the terra firme forest. During this study, three herds used the eastern portion of the island (east of the two inland lakes, Fig. 6-3b). Two used the central Sapotaceae rich area, while the third used the eastern tip of the island. That tip area has an <u>Astrocaryum</u>-rich version of the terra firme forest (unpublished transect data), and adjacent to it a very large <u>Pradosia</u> dominated forest which seems to

be related to the _Peltogyne_/_Pradosia_ community found on the southeastern shore of the island (floristic plots 20-25; pers. obs.). Thus, all three herds had access to a _Pradosia_ rich area (terra firme forest) and a palm rich area (river forest), which they used seasonally (Fragoso unpublished data). They remained within one forest type for several weeks, and stayed at single tree patches for several days (pers. obs.). They used _Astrocaryum_ pulp more frequently than white-lipped peccaries. Collared peccaries may be responding to the landscape at the tree patch scale, focusing on monodominant tree species areas within terra firme forest and moving among them. Sapotaceae and palms would still provide pulp at different times of year, since _Attalea_, _Astrocaryum_ and _Pouteria_ spp. are all temporally displaced from each other in peak fruiting time. _Pradosia_ may be a key food for collared peccaries, because like _Mauritia_ different patches fruit asynchronously (pers. obs., Nuñes 1992).

Agouti scale

Agouti home range sizes match the tree-patch scale, while agouti grain size is at the individual tree scale. What is a Sapotaceae-rich area to white-lipped peccaries is a high diversity area to the agoutis and provides them with food year round. Diversity enters into the agouti scale from two sources. First, 50 m segments in the terra firme habitat had more than one fruiting species per segment (Table 6-3),

indicating that despite dominance by one species, individual trees still provided variation in the species available. Agoutis could therefore select home ranges on the individual tree scale, choosing enough inter-tree variation to provide food year round (c.f. Chapter 5). Second, in the area where two or more species patches come together, diversity and abundance will be high. Home ranges centered around these boundaries would have the highest availability of food. Nevertheless, individual agoutis may be at a higher risk than either peccary species of experiencing seasonally decreasing food availability, due to the clumping of food rich and food poor areas at the 150 meter scale. Food hoarding may be a necessary behavior to mitigate this spatial unpredictability. Conversely, hoarding may ensure the availability of high quality foods year round, even when lower quality foods are available.

Other fruit-eating species on Maracá

Spider monkeys use different fruit species than the terrestrial mammals in this study, and consequently should perceive a different pattern of resource distribution. The core areas in the home range of one group (Nuñes 1992), whose range overlapped the Trail 2 transect in this study, corresponds to concentrations of Spondias and Pradosia trees in the center of their range and Tetragastris and Brosimum trees on the edge (pers. obs.). During Nuñes (1992) study

the group was confined to terra firme forest, and did not use
Mauritia wetlands, although I observed the same group three
years later feeding on Euterpe precatoria fruit in a Mauritia
strand; Euterpe seeds were common at spider monkey defecation
sites on the trail system (sites under sleeping trees where
feces become concentrated). A group with 24 animals had a
316 ha home range, smaller than the home range of a similarly
sized group of collared peccaries.

In her 1981-82 study of tortoises, Moskovits (1985,
1998) documented an aggregated pattern of fruiting trees
similar to that found for the two terra firme transects in
this study. Her study site also overlapped with those for
the agouti and spider monkey studies. She monitored one
trail parallel to my Trail 2 and one perpendicular to it,
both 2 km long, and documented fruiting tree aggregations at
approximately 150 meter intervals. Tortoises used
Sapotaceae, Mauritia, and Annonaceae fruits. Annonaceae
trees co-occur with Attalea and Astrocaryum in my study
sites, providing an alternative food for tortoises, which did
not feed on those two palm species.

Implications for Habitat Partitioning, Competition, and
Community
  Structure

Because the five species discussed above either use
different species or perceive availability of the same

species differently, fluctuations in food availability should differ for them. Their own populations could therefore fluctuate out of synchrony with each other, except when massive fruit failure affects all of them, as occurs during El Niño years and other extreme droughts. Out of phase fluctuations, and fluctuations at different temporal scales, would tend to reduce competition among fruit-eating species.

This study also suggests that in Neotropical forests, it is the abundant tree species, rather than keystone species sensu Power et al. (1995) that set carrying capacity and determine food availability patterns. Across the Amazon, common trees in the Sapotaceae and Palmae appear to be staple foods for fruit-eaters, especially large terrestrial mammals (Bodmer 1989, Fragoso 1994). An understanding of the distribution of species in these families may add to our understanding of animal diversity patterns in the region.

Table 6-1. Scale of habitat use by the tree different animal species considered in this study. All home range sizes are derived from on-site studies.

| | | Grain Size | Scale | |
Species	Food Patch Size	Daily Range (area and linear distance)	Home Range Size	Refs.
Agouti	One tree	1-2 ha 150-200 m	.03 - .08 km^2 (3-8.5 ha)	This study Chpt. 5
Collared peccary	Large tree or group of fruiting trees	10 ha 1 km	10-15 km^2 (1000-1,500 ha)	Fragoso 1998
White-lipped peccaries	One habitat type	200 ha 5-10 km	20-150 km^2 (2000 - 15,000	Fragoso 1998

grain size = a) what is perceived as a food patch; b) area assessed over the short term (daily or near daily) for foraging decisions, or distance moved in one-two days between two food patches.

scale = area which the individual or herd assesses over the long term (one seasonal cycle or other relevant sub- or supra-annual cycle for the study area).

Table 6-2. Abundances of key food species for peccaries and agoutis in floristic inventories carried out on Maracá Island Ecological Reserve by Milliken and Ratter (1989) and Nascimento (1994). A (-) signifies no data available. From left to right, species are: Pradosia surinamensis, Pouteria surumuensis, Pouteria hispida, Pouteria venosa, Ecclinusa guianensis, Astrocaryum aculeatum, Attalea maripa, Lecythis corrugata, Tetragastris panamensis, Brosimum sp., Hymenea sp (courbaril and parvifolia), Licania kunthiana, Oenocarpus bacaba, Enterolobium sp. (schomburgkii and cyclocarpum). One key species discussed in the text did not have data in any of the plots: Couepia sp. Plot numbers correspond to those shown on Figure 6-3a.

Quad #	Pr s	Po s	Po h	Po v	Ec g	As a	At m	Le c	Te p	Br sp	Hy sp	Li k	Oe b	En sp
1	14	13	6	0	5	6	14	4	5	7		3	0	1
2	13	9	16	2	5	8	3	8	34	21	1	10	0	0
3	0	5	0	-	1	8	0	4	2	8	0	6	0	0
4	0	1	0	-	1	9	1	4	3	11	0	11	0	0
5	2	0	0	-	3	8	0	7	7	4	0	5	0	0
6	4	0	1	0	0	1	5	3	1	0	0	0	0	0
7	8	1	2	0	24	0	7	13	0	0	1	0	0	0
8	3	6	0	0	19	0	3	15	0	1	0	0	0	0
9	10	4	1	-	8	2	10	8	1	2	0	9	-	0
10	8	1	2	-	11	2	1	9	1	5	0	16	-	0
11	7	1	0	-	15	2	7	4	10	0	0	10	-	0
12	12	4	1	-	12	0	1	7	19	1	0	2	-	0
13	5	1	2	-	6	0	22	10	4	0	0	1	-	0
14	8	0	13	-	16	4	1	20	14	10	0	20	-	0
15	9	1	0	-	1	0	17	4	0	0	0	0	0	
16	19	1	0	-	4	0	7	5	0	0	0	0	0	-
17	8	1	7	-	41	1	4	22	0	0	0	3	0	-
18	2	9	5	4	0	0	2	0	4	2	0	2	2	0
19	1	0	0	0	3	0	2	0	14	1	0	5	21	1
20	12	7	0	-	6	0	0	0	0	0	0	0	0	0
21	11	1	0	-	1	0	0	0	0	0	0	0	0	0
22	24	1	0	-	1	0	0	0	0	0	0	0	0	0
23	20	5	0	2	1	0	0	0	0	0	0	0	0	0
24	0	2	0	0	0	0	0	0	0	0	0	0	0	0
25	2	6	1	0	1	0	3	0	3	0	0	0	0	0
26	1	3	1	1	0	0	5	3	5	1	0	0	0	0
27	0	2	2	1	1	0	2	0	1	3	0	0	0	0
28	1	1	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	1	2	0	0	5	0	0	8	1
30	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Table 6-3. Total fruit availability in three different
habitat types (including all species, not just "edible"
species).

	Habitat		
Variable	River Trail	Trail 2	Km 7
Total Species	42	50	63
Mean (range) # species/run	8.6 (6-15)	14.4 (9-20)	13.9 (11-19)
Mean (range) # fruit patches /run	36.7 (14-65)	37.1 (18-63)	32.7 (16-56)
Mean (range) # patches/ species	4.5 (2.4-9.8)	2.6 (1.7-4.2)	2.4 (1.3-4.10
Mean (range) # empty 50 m segments/run	18.7 (7-28)	17.4 (7-29)	19 (11-30)
Mean (range) edible species per segment	1.68 (0-3)	3 (0-6)	3.23 (1-7)

Figure 6-1. Location of Maracá Island Ecological Reserve.
Adapted from Milliken and Ratter (1998).
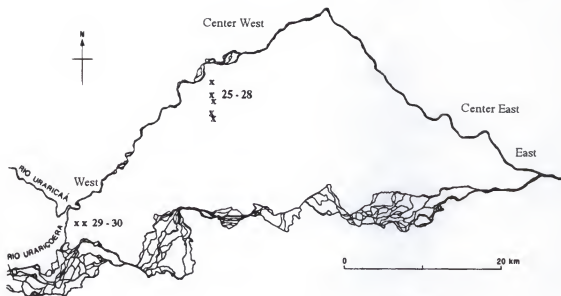
Figure 6-2. Overview of Maracá Island Ecological Reserve,
showing the general location of floristic plots in the east
and center east, and the specific location of the plots in
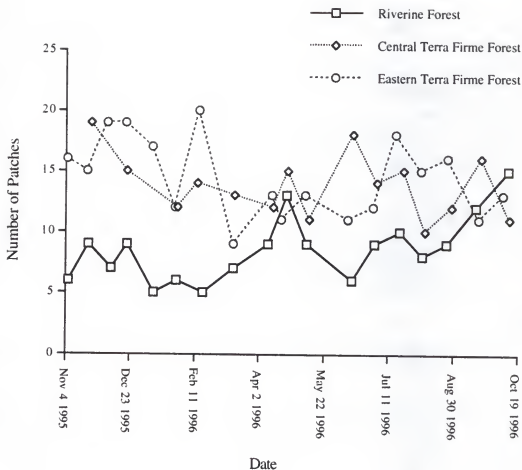the west and center west.

0   Metres   10000

Furo Santa Rosa

N

×18

8 × ×7

12 ×
× 15-17
13 ×14 × ×
×19   ○ 9-11
            Trail
                    1 ×× 2
                    × ×× 3-5
                    6 ×

24 × 23
× ××× 20-22

Furo Maracá

▭ wlp herd 1

▥ wlp herd 2

River Trail
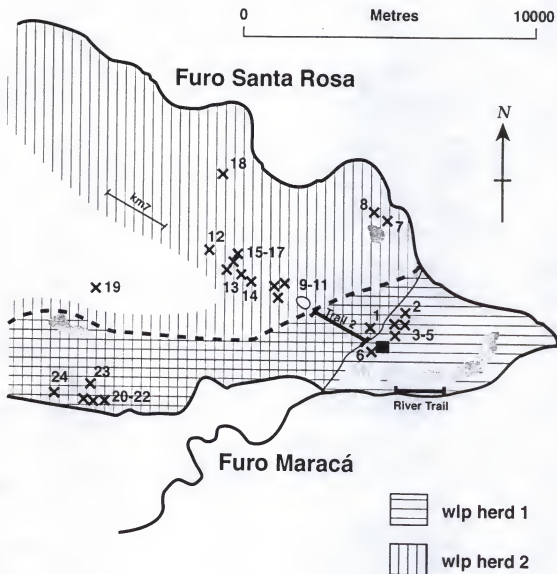
a)

Figure 6-3. Floristic plots and peccary home ranges on the
east and center east portions of Maracá Island Ecological
Reserve. a) White-lipped peccary home range (1995-97),
phenology transect and floristic plot locations. b) Collared
peccary (995-98) and white-lipped (1991-93) peccary home
ranges

Furo Santa Rosa

0   Metres   10000

N

	cp herd 1
	cp herd 2
	cp herd 3
	wlp herd 3 (1991-92)

Furo Maracá
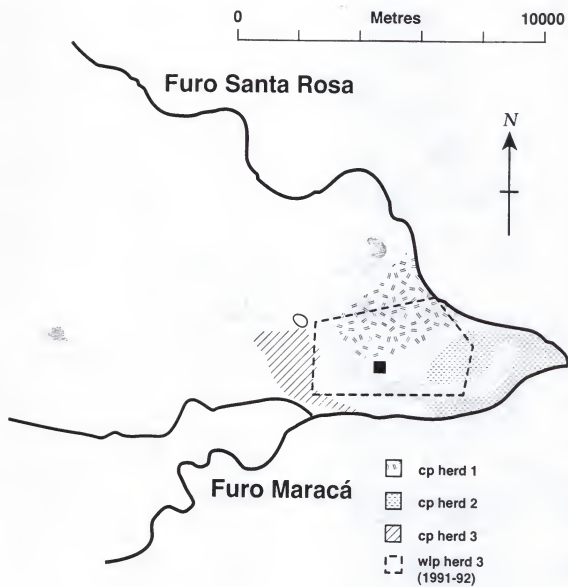
b)

Figure 6-3, continued

a)

Figure 6-4. Patterns of total fruit availability on the
ground on each of three transects from November 4 1995
through October 13 1996. a) number of species of fruits and
seeds, b) number of patches of fruits and seeds, c) mean
number of patches per species, and d) number of empty
segments encountered on each run. Note that three runs are
missing from Km 7 in central terra firme forest compared to
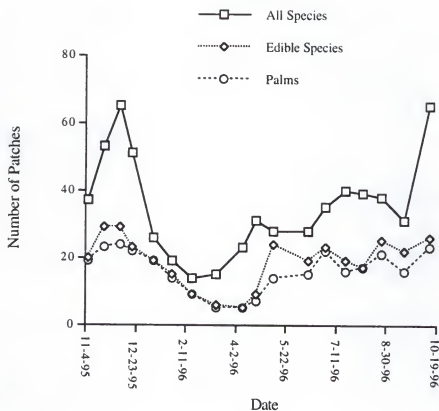Trail 2 in eastern terra firme and the River Trail.
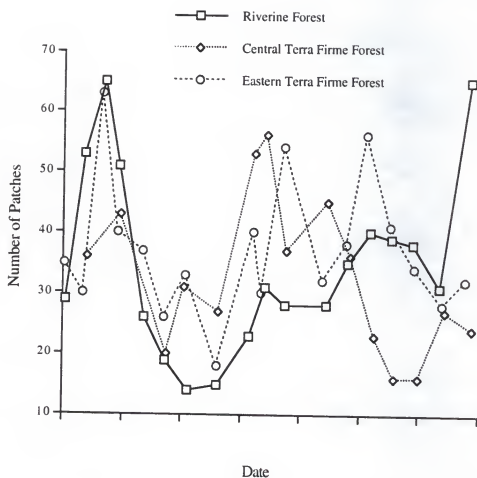
b)

Figure 6-4, continued. Dates as in a).
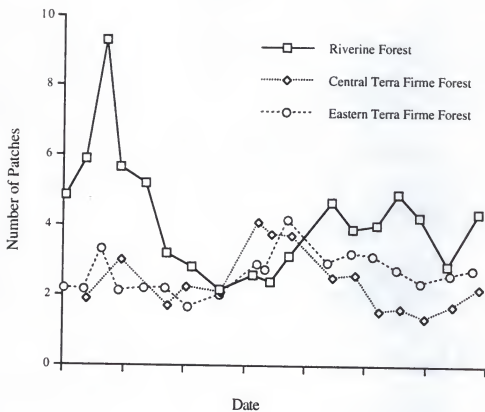
c)

Fig. 6-4, continued. Dates as in a).
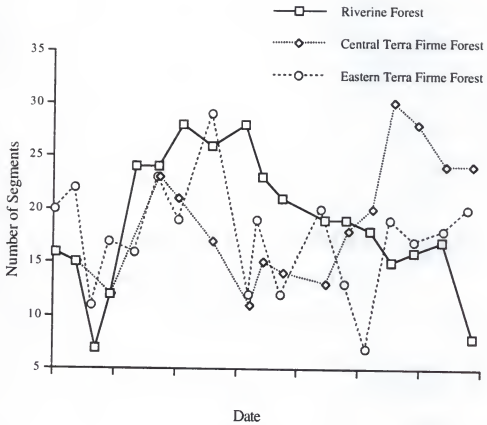
d)

Figure 6-4 continued. Dates as in a).

a)

Figure 6-5. Comparison of temporal availability of all fruit species, all edible fruit species, and the contribution of all edible species, palm species, and sapotaceae species to overall fruit availability on each of three transects from November 4 1995 to October 13 1996. a) Trail 2. b) Km 7. c) River Trail
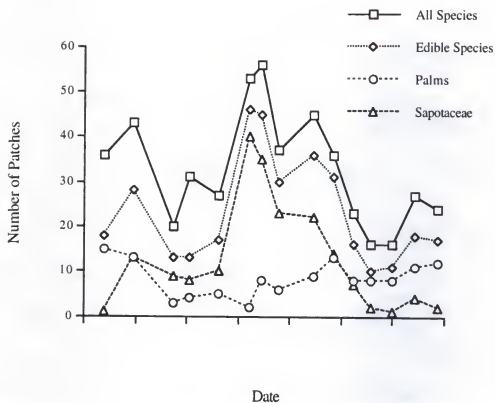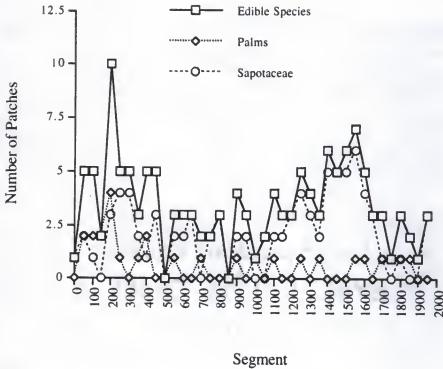
b)

Figure 6-5, continued. Dates as in a).
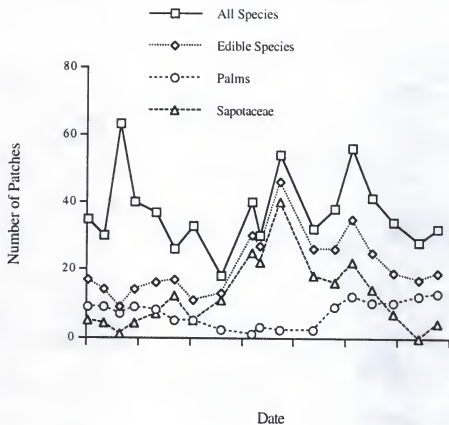
c)

Figure 6-5, continued. Dates as in a)

Segment

a)

Figure 6-6. Spatial pattern of availability of edible fruit species on three 2-km long trails divided into 50 meter segments. a) Trail 2, b) Km 7 and c) River Trail. Presented is the maximum number of patches of each edible species available during any one sample of the transect, summed across species. See text for explanation.
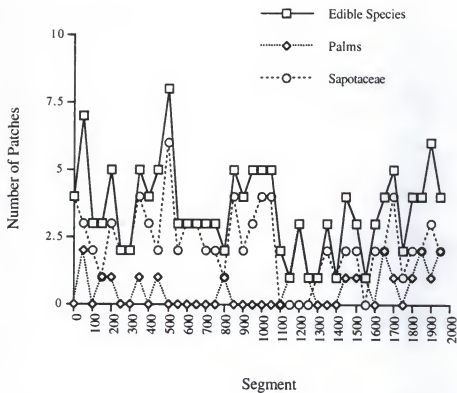
Segment

b)

Figure 6-6, continued.
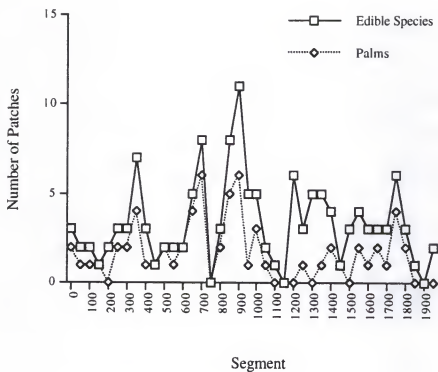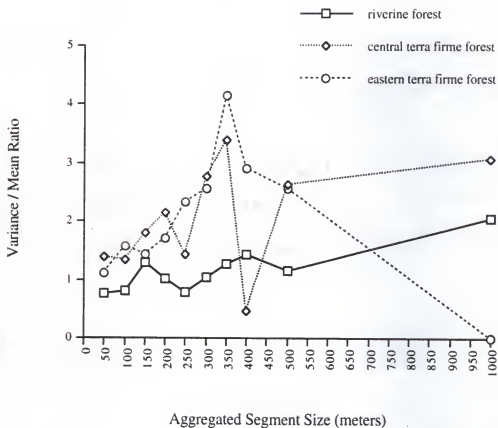
Segment

c)

Figure 6-6, continued.

Figure 6-7. Index of dispersion (variance/mean) for the original 50 x 3 meter segment sizes and subsequent aggregations of segments to yield 100, 150, 200, 250, 300, 350, 400, 500 and 1000 meter segments.

CHAPTER 7
CONCLUSIONS AND IMPLICATIONS

Phenology: Methods and Implications

There has been discussion in the literature (Zhang and
Wang 1995) and at recent meetings (e.g., phenology symposium
at the 1998 meeting of the Association for Tropical Biology)
about the quality of information yielded by different methods
of describing fruit production patterns. This study relied
on the use of a patch-based index for the evaluation of food
availability and patterns of fruit production. Two-kilometer
long un-raked transects were walked every two to three weeks
and the identity and number of fruits, seeds, and
germinating seed patches counted. The method proved
successful in detecting the overall seasonal pattern of fruit
production at the study site, as shown by comparison with two
studies that used a traditional canopy count method to
describe phenology. It was also successful in detecting
differences among sites in the diversity of fruit species
available to consumers, and in spatial (aggregated vs.
dispersed) and temporal (seasonal and supra-annual) patterns
of fruit availability.

Analysis in this study concentrated on the spatial
distribution of fruit patches and the relative levels of

fruit productions compared among different habitats. For this type of data, it was an effective, low disturbance method, which can be used when more detailed information is not required or already available from previous studies. It would also serve as a rapid way of monitoring supra-annual changes in fruit fall patterns and availability levels.

Given the frequency of supra-annual variation in fruit production and diet, the current study was limited by its one and a half year time frame. However, the same major items-- Sapotaceae and palm fruits--were used by collared and white-lipped peccaries at the same site during studies separated by three years (Fragoso 1994). Additionally, studies at other sites, especially in Central America, show a remarkable similarity in the diets of at least agoutis (Smythe et al. 1996, Naranjo unpublished data). The importance of Sapotaceae and Palmae at these sites, and their importance also to ungulates in the Peruvian Amazon (Bodmer 1989) suggest that both families have a long history of ecological and evolutionary interactions with terrestrial fruit and seed eaters, and that the Sapotaceae in particular require more careful study in terms of their distribution and role in mammalian community structure.

Palm-Mediated Bruchid-Vertebrate Interactions

Although Janzen (1971) suggested early on that palm seed consumers may be feeding on bruchid beetle larvae rather than

endosperm, subsequent researchers did not follow up on the inplications of this observation for frugivore-granivore diets. This study indicates that white-lipped peccaries on Maracá rely almost exclusively on beetle larvae and seldom ingest endosperm. Agoutis and squirrels, on the other hand, ingest varying amounts of both kinds of endocarp content. The spatial distribution of endocarp piles used by each species suggests that white-lipped peccaries visit palm-rich habitats as part of their seasonal use of a large scale mosaic, whereas squirrels used the palm seeds and larvae as a staple year round. Agoutis, in contrast, used the seeds and larvae as a non-preferred food when preferred food items are not available. Variation in availability was spatial during this study, but may also be temporal due to years of low forest-wide fruit availability.

Complexity in Frugivory Systems

Figure 7-1 illustrates the participants in the _Attalea maripa_ frugivory system described to date on Maracá. At the largest scale, environmental factors act both on the palm (affecting the level of fruit production) and on the interactions between fruits and animals (consumers are more likely to use palm pulp and/or endocarp contents in some habitats and seasons than in others) (Chapter 4). Seed dispersal, a consequence of animal feeding, afects habitat type by providing an input of seeds that may create new palm

patches or maintain existing populations (Fragoso 1997b). At the smallest scale, pulp removal by different consumers affects oviposition by bruchid beetles (Chapter 3). In some cases, different oviposition patterns will translate to different infestation rates. The presence of different consumer species in different habitat types where the palm occurs could translate to different oviposition patterns in different environments. That is, since the distribution of consumers and consumer feeding behavior is patchily distributed over the landscape, this patchiness may superimpose patterns of seed mortality and result in aggregated tree distributions at the scale of hundreds of meters to tens of kilometers.

The activities of different dispersers also affect pattern due to variation in the degree of protection afforded to the dispersed seeds (in this case protection from bruchid beetles). In the _Attalea_ system, agoutis and primates do not remove seeds from the area of heaviest bruchid activity (Chapter 3, Fragoso 1997). Long-distance seed dispersal by tapirs, on the other hand, reduces predation by bruchids, both by placing palm seeds in a palm and beetle poor habitat and by protecting them with fecal matter (Fragoso 1997b, Fragoso unpublished data). Referring back to Figure 7-1, it is possible that long distance dispersal also affects parasitism by wasps on bruchids, if parasitism rates by the Hymenopteran parasites are also habitat specific.

With respect to the evolution of fruit trais, it is plausible that the thick endocarp of _Attalea_ palms is a response to predation pressure by vertebrates. Fragoso (1994) suggests that bruchid beetles exert selection on seed number rather than endocarp thickness, given the beetles' ability to penetrate all endocarp thicknesses for the Maracá population. In fact, it is plausible that _Attalea_ did not become potential hosts for bruchid beetles until their endocarps were thick enough to provide protection for the developing larvae. Such protection is necessary to reduce predation by vertebrates and possibly parasitism by Braconid wasps, which must also penetrate the endocarp with their ovipositor to lay their eggs on bruchid larvae.

A comparison of fruit size, endocarp thicknes, and seed number for the approximately 27 species currently placed in the _Attalea_ palm group might shed some light on the evolutionary response of the palms to different selection pressures on fruit traits. One member of the _Attalea_ genus ("babassu", _Attalea speciosa_) has large fruits with extremely thick endocarps and four to six rather than one to three seeds per endocarp (Henderson 1995). _Attalea tessmannii_ produces even thicker endocarps (based on diagrams and comments in Henderson 1995), but only three seeds per endocarp. One study in Pará, Brazil, suggests that rodents cannot penetrate the _Attalea speciosa_ endocarps (Anderson et al. 1991). It is also unlikely, based on the data from Maracá, that white-lipped peccaries would ever crack the

endocarps for $\underline{A}$. tessmanni and $\underline{A}$. speciosa. A systematic comparison of consumer sets, environmental conditions, relative palm abundances, and intensity of predation by bruchid beetles could help tease out some of these complex interrelations. At this point in time, however, the required information is available for only three or four species in the Attalea group.

Current ecological processes can account for some of the dispersal-and survival-related features of Attalea maripa. Thus, the endocarp allows escape from bruchids; the pulp attracts tapirs (Attalea maripa has a high protein content and low fiber content relative to other palm species in the same habitat type; Castellanos and Chanin 1996), which feed on uninfested fruits; the seeds can survive predation by white-lips; and the seedling can survive fire and grazing (Anderson et al. 1991, Fragoso and Silvius unpublished data). From the palm's "point of view," rodents and primates at present do not appear to play a biologically significant role in the system, although they may at times increase infestation rates of seeds by bruchid beetles through pulp removal (Chapter 3). One possible exception is seed dispersal by spider monkeys (Ateles sp.). In the Orinoco basin of southern Venezuela, Castellanos and Chanin (1996) noted that Ateles belzebuth dispersed Attalea maripa seeds to defecation sites under sleeping trees in areas of low adult Attalea density, and that seedling density was high at those

sites. This could be a situation similar to that described by Fragoso (1997b) in northern Brazil.

Our interpretation of this and any other frugivory systems, however, is limited by the processes that we currently observe. Selective pressure by currently unimportant consumers or environmental phenomena may have affected the palm in the past, and created the phenomena we see today. We could therefore also expect that current ecological processes are affecting future fruit traits and palm distribution patterns. Recent work in French Guiana (Brunner et al. 1998) with the palm <u>Astrocaryum sciophillum</u> indicates that a juvenile palm may be nearly 200 years old before its stipe (meristem) emerges from the ground. This means that by the time an individual palm of this species reaches reproductive age, the processes and even some environmental conditions may have changed drastically from the time when it was first dispersed as a seed. While it is unlikely that many palm species have such a drastically delayed growth pattern, the example of <u>Astrocaryum sciophillum</u> serves as an important caution that we need to expand our historical perspective when interpreting ecological patterns.

<u>Mosaics of Fruit Availability: Scale and Grain Size</u>

The understanding gained from walking through a forest in which one knows the habitat preferences of certain animal

species is very different from the understanding gained from walking through a forest in which one knows the home ranges of individually distinguishable animals. The first kind of information provides averages and eliminates exceptions, thus emphasizing pattern. The second kind of information points to the ways animals make choices, thus emphasizing process. Both types of information may be key to our understanding and management of tropical fruit- and seed-eating animal communities.

The work of Terborgh et al. (1990) clearly demonstrates the value of the second kind of knowledge described above. The authors created a layered map of the home ranges of individuals of several bird species in 97 hectares of lowland forest in Amazonian Peru. The study yielded important insights into the nature of scientific measurements of species richness. In particular it showed that small sample plots underestimate richness because they miss individuals or species with large territories (note that these are not necessarily rare species, they just move a lot with respect to the observer).

The study also described how patchiness in forest habitat structure contributes to animal species richness, when richness is measured at a large enough scale. The maximum number of species overlapping at any one point in the study site was 160, yet a total of 319 species were identified in the entire study site. There are two possible explanations for this result. First, some species may have

used the habitat at a larger spatio-temporal scale than measured in the three month study, rotating between habitats on an annual or supra-annual basis. Second, different species may have been restricted to different sites or habitats within the plot for either environmental reasons (food / shelter availability) or behavioral reasons (aggression / exclusion between species).

Fruit and seed production by individual tree species or within habitat types or species communities is not constant year round in Neotropical forests (van Schaik et al. 1993, Leigh et al. 1996). Fruit and seed eating animals therefore need an environmental mosaic in order to survive. The nature of the mosaic will depend on the scale of activity of the animal species. As shown for the same Peruvian study site described above, a territorial ground-dwelling frugivorous bird, the white-winged trumpeter (<u>Psophia</u> <u>leucoptera</u>), established home ranges in areas larger than required to provide food during the season of high fruit availability. but large enough to provide food during the season of fruit shortage. At the trumpeters' scale of activity (approximately 70 hectare territory, or 0.7 km^2), either individual trees, tree patches or small-scale edaphic gradients (in this case the old Manu river flood plain) could provide the mosaic of food availability, depending on the grain size used by the animal. A smaller animal, with a smaller home range size, might perceive or encounter only the tree patch or individual tree level of variability, while a

much larger animal might encounter large-scale edaphic gradients and a sharply segregated habitat mosaic.

Such a differential perception of the environmental mosaic could play a role in the coexistence of species with similar diets, such as white-lipped peccaries, squirrels and agoutis. Temporally shifting use of small areas by the largest, more mobile species, would reduce their period of overlap with the home ranges of individual, smaller animals. The nature of the horizontal habitat mosaic (as opposed to vertical forest structure) could thus influence species diversity, when it is measured at a large enough scale. This brings us back to the conclusions of Terborgh et al.'s (1990) study, which hints at the irrelevance of alpha diversity measures for patchy habitats. If communities are spatially structured by means of body size/home range size segregation, then small-scale measures of community structure, such as alpha diversity, will say little about the processes that structure such communities.

Plant-Animal Interactions and the Aggregated Distribution of Tropical Forest Plants

The high floristic heterogeneity on Maracá, though undoubtedly influenced by the island's location near the forest-savanna boundary, is probably typical of other Amazonian sites, as indicated by studies of habitat heterogeneity in Peruvian rain forest (Tuomisto et al. 1995), and habitat descriptions of other transitional Amazonian

forests (Peres 1994, Peres and Baider 1997). For example,
the decrease in palm abundances from east to west may be
related to the increasing distance from the forest-savanna
boundary, an active disturbance edge that probably favors
palm establishment (see below).

Lieberman and Lieberman (1993) reviewed the literature
on plant distribution data from floristic plots until 1986.
They cite only one plot-based floristic inventory in
Amazonian forest, but describe nine other sites in wet and
dry tropical forests. All studies, except the one in
Amazonian forest, showed a predominance of clumped
distributions for abundant tree species.
Most plot studies to date have been carried out in small
plots of less than 4 ha in extent; only three covered areas
of between 10 and 20 ha. Since then, larger floristic plots
(50 ha) have been established at several Neo and Paleo-
tropical forest sites (Condit 1995, Foster and Hubbell 1990).
Data from one of these sites, in Borneo, analyzed at several
quadrat sizes, shows clumping at the largest scale studied
(He et al. 1996). Interestingly, it shows an aggregated
distribution of species diversity and richness across the 50
ha site, as a result of the non-random distribution of
individual species. At a smaller scale, early work on Barro
Colorado Island, Panama, showed aggregated patterms at the 5
hectare, 1 hectare, and quarter hectare quadrat sizes
(Thorington et al. 1996). Clumping at such scales (50
hectares and below) is biologically interesting from the

point of view of plant dynamics and small animal responses. In Neotropical forests, however, the home ranges of most fruit-eating species larger than a paca (_Agouti paca_) are much larger than 50 ha, and studies at larger scales are required for understanding of food availability patterns for such animals.

Much of the clumping or patchiness in tropical forest plant distribution patterns can be explained by edaphic factors (soil type, drainage conditions and topography). In several studies the distribution of particular plant species or plant associations have shown strong correlations with such factors (Tuomisto and Ruokolainen 1993, Tuomisto et al. 1995, Clark et al. 1995, 1996, Steege 1993). These correlations transcend taxonomic boundaries, and have been examined in detail for legumes (Steege 1993), palms (Kahn and Castro 1985, Kahn and Mejia 1990, Clark et al. 1996), and melastomes (Tuomisto and Ruokolainen 1993). These correlations also occur at several different scales—in transitions over a few meters between sand and clay soils (Tuomisto et al. 1995), along slopes with changing drainage qualities (Steege 1993), and across landscapes at the tens to thousands of kilometers scale (Tuomisto et al. 1995). On Maracá itself, the transition in species identity from east to west depends to a large extent on the shift in substrate type (Milliken and Ratter 1998).

Having said all this, several of the above studies have found variation in plant distribution that cannot be

explained by measured edaphic factors. In all cases, the unexplained variation occurs within clay soils. Both Tuomisto et al. (1995; and unpublished data in Condit 1996), and Steeger (1993) found that although white sand soils supported characteristic plant associations, with predictable species dominance, and although plant associations on sandy soils were easily distinguishable from those on "brown sand" or "clay" soils, much variation occurred within the clay soils that was not predictable based on measured factors. In Guayana, Steege (1993) found that species dominance varied greatly in different areas of "brown sand" soils. In Peru, species composition on clay soils was also variable (Condit 1996). He et al. (1996) found that on the 50 hectare plot in Malaysia, much variation in diversity and distribution patterns at the smallest scales could not be explained by edaphic factors, and the authors felt that biological processes occurring at these scales were most likely responsible for the resulting patterns.

It is in these soil types and at these scales that the effect of seed dispersal and seed predation processes may be most visible in plant distribution (e.g., the clumped distributions of _Attalea_, _Ecclinusa_ and _Oenocarpus_ in this study). The short distances characteristic of seed dispersal by agoutis may create clumped patterns (c.f. Peres and Baider 1997) or maintain a clumped pattern initially created by disturbance or other historical accident. Plant-animal interactions may also affect plant distribution along edaphic

gradients, as animals react to food availability on different soil types, but it is more difficult to tease out such processes against the background of correlated edaphic factors. The following hypothetical examples illustrate how such processes could be operating on Maracá.

Several botanical workers have noted that on Maracá the _Attalea_ _maripa_ palm frequently occurs in aggregations around wetlands within the forest, or on slopes leading down to seasonal streams. They proposed that this is due to soil and drainage conditions favored by the palms (Milliken and Ratter 1989). However, _Attalea_ fruits are a preferred food for tapirs, which ingest the fruits intact and defecate thousands of viable seeds in latrines (Fragoso 1997b). Since tapirs preferentially defecate in wetland sites even in the seasons when these are dry, many _Attalea_ seeds are carried to the very sites where _Attalea_ is commonly found.

How to distinguish between the hypotheses that dispersal by tapirs or edaphic conditions control the final distribution of _Attalea_? On Maracá, tapirs exhibit the unusual behavior of defecating in upland latrine sites, at the base of buttressed emergent trees (Fragoso 1997b). Dense aggregations of seedlings and saplings occur around these latrine sites, indicating that there is higher seedling survival here than around parent trees or at random sites in the forest (Fragoso 1997b). Thus the same process--dispersal by tapirs--can account for the location of _Attalea_ in both upland and wetland sites. Soil and drainage conditions

differ between upland and wetland sites, and therefore do not have the same explanatory power as dispersal.

A second, scale-dependent example from the same frugivory system involves a comparison of two frugivores with different home range sizes, acting on the same tree species. Tapirs are the primary dispersers of _Attalea_ seeds on Maracá (based on number and survival rate of seeds moved). Contrary to paradigm-based expectations (Foster 1986, Foster and Janson 1985), this large-seeded, slow to mature tree appears to be a colonist or edge and disturbance specialist. When the forest is cleared, due to a combination of high dispersal and high seedling survival, _Attalea_ establishes monodominant stands. _Attalea_ and other large-seeded palms are resistant to fire and grazing--their hypocotyl grows downward first before turning to the surface, ensuring that the meristem is protected underground (Anderson et al. 1991, Brunner 1998, Tomlinson 1990). _Attalea_ is also commonly found along natural forest-savanna boundaries. Its competitive ecology and habitat preferences cause it to be densely concentrated in a narrow strip along habitat edges. On Maracá, this corresponds to the riverine forest. Tapirs come to the riverine forest specifically to feed on _Attalea_ fruits, ingesting hundreds of ripe fruits from the ground from several trees during one foraging bout. Because tapirs have long gut retention times (Bodmer 1989) and large home ranges, they carry seeds from the river edge into the terra firme forest several kilometers away. Due to high survival of tapir defecated seeds, this

could broaden the strip along which _Attalea_ occurs. On
Maracá, in places where there is little _Attalea_ near the
river, there is correspondingly little _Attalea_ in the
interior forest. Agoutis, frequently cited as the best
dispersers for palm seeds (Chapter 5), operate at too small a
scale to account for _Attalea_ dispersal into the forest. With
home ranges of about 4 hectares (Chapter 5), they cannot
create a bridge between river forest and terra firme forest
the way tapirs do.

In yet another example from Maracá, home range size
interacts with pre-existing vegetation patterns to intensify
a vegetation gradient. Several fruit species (_Licania_
kunthiana, _Pradosia_ _surinamensis_, _Ecclinusa_ _guianensis_,
Tetragastris _panamensis_ and other species in the Burseraceae)
used by spider monkeys co-occur with _Peltogyne_ in the central
monodominant forests. During a six month transect study
(Mendes-Pontes 1995) spider monkeys were the only primates
seen with any frequency in the _Peltogyne_-dominated habitat.
Peltogyne itself has no known seed or seedling predators on
Maracá, other than leaf cutter ants (_Atta_ sp.), and no known
dispersers (Nascimento 1994). In other words, with the
exception of spider monkeys, the _Peltogyne_ forest is a fairly
hostile environment to fruit and seed eating vertebrates.
The habitat is extensive enough that only white-lipped
peccaries can easily move across it in a day and include the
area in their home range. All other fruit eating species
would face severe seasonal and probably sub-seasonal food

shortages in this habitat. In the absence of fruit eating species, the _Peltogyne_ forest also becomes a barrier to seed dispersal, and may contribute to the turnover in species composition from east to west on the island. The vegetation transition is sharpest at precisely the location of the _Peltogyne_ area (Milliken and Ratter 1989, 1998); since it also coincides with a geomorphological transition, it is difficult to tease apart the two alternative explanations for the vegetation turnover.
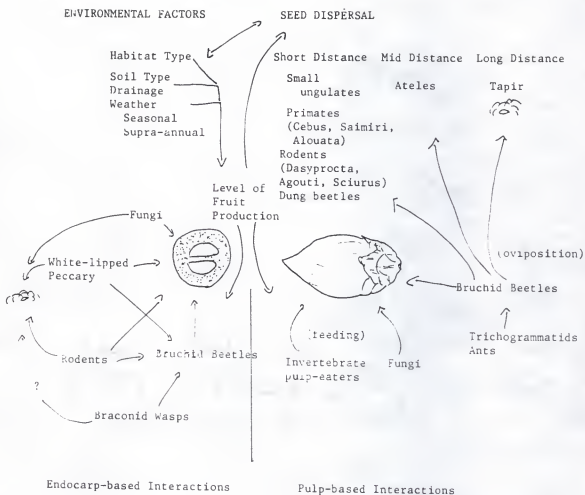
Figure 7-1. Complex interactions among biotic and abiotic factors in the _Attalea_ _maripa_ system on Maracá. See text for explanation.

APPENDIX I
"EDIBLE*" PLANT SPECIES ON PHENOLOGY TRANSECTS

Family	Species
Anacardiaceae	*Spondias mombin*
Annonaceae	*Duguetia guianensis*
Burseraceae	*Tetragastris panamensis*
Caryocaraceae	*Caryocar sp.*
Chrysobalanaceae	*Licania kunthiana*
Chrysobalanaceae	*Couepia sp.*
Icaniaceae	*Leretia sp.*
Lecythidaceae	*Augusta suberba*
Lecythidaceae	*Lecythis corrugata*
Lecythidaceae	*Couratari multiflora*
Leguminosae	*Hymenea parviflora*
Leguminosae	*Hymenea courbaril*
Leguminosae	*Enterolobium sp.*
Leguminosae	*Swartzia dipetala*
Leguminosae	*Andira inermis*
Moraceae	*Bagassa surinamensis*
Moraceae	*Brosimum sp.*
Moraceae	*Ficus sp.*
Myristicaceae	*Virola surinamensis*
Myristicaceae	*Virola sp.*
Palmae	*Oenocarpus bacaba*
Palmae	*Attalea maripa*
Palmae	*Astrocaryum aculeatum*
Palmae	*Astrocaryum mumbaca*
Palmae	*Euterpe precatoria*
Palmae	*Mauritia flexuosa*

Family	Species
Passifloraceae	*Passiflora sp.*
Rubiaceae	*Duroia eriopila*
Rubiaceae	*Genipa americana*
Sapotaceae	*Chrysophyllum sp.*
Sapotaceae	*Pouteria venosa*
Sapotaceae	*Pouteria hispida*
Sapotaceae	*Pouteria surumuensis*
Sapotaceae	*Pradosia surinamensis*
Sapotaceae	*Pouteria sp.*
Sapotaceae	*Pouteria sp. "abiu"*
Sapotaceae	*Sapotaceae sp.*

*"Edible" species are those known or expected to be be eaten by agoutis, white-lipped peccaries and collared peccaries, based on studies at Maracá (Fragoso 1994, Silvius this study) and reports in the literature for other Neotropical sites.

FLORISTIC PLOT DATA SUMMARIZED FROM MILLIKEN AND RATTER
(1989) AND NASCIMENTO (1994)

Plot #	Ref.	Habitat	Area (ha)	# Spp	# Trees	Trees/ ha	H'	J
1	M+R	Tall mixed terra firme forest, eastern plateau	0.369	54	200	504.61	3.567	0.894
2	M+R	Tall mixed terra firme forest, eastern plateau	0.519	51	200	385.09	3.271	0.832
3,4,5	M+R	Tall mixed terra firme forest, eastern plateau	0.75	80	597	408.9	3.61/3 .37+/- 0.14	0.824/ 0.9+/- 0.02
3	N	Tall mixed terra firme forest, eastern plateau	0.25	41	117			
4	N	Tall mixed terra firme forest, eastern plateau	0.25	41	107			
5	N	Tall mixed terra firme forest, eastern plateau	0.25	45	117			

Plot #	Ref.	Habitat	Area (ha)	# Spp	# Trees	Trees/ha	H'	J
6	M+R	Angico forest (marginal form of typical terra firme forest on the eastern end, on a steep slope leading down to campo)	0.103	31	56	541.42	3.266	0.951
7	M+R	Tall mixed terra firme foreste, with campina influence	0.129	22	80	622.3	2.447	0.792
8	M+R	Mixed terra firme forest on sandy soil, depaupa-rate with marginal and colonizing speices	0.25	30	149	596	2.706	0.796
9,10, 11	N	Terra firme forest without Peltogyne	0.75	31 +/- 2.89	309		3.02 +/- 0.08	0.88 +/- 0.01
9	N	Terra firme forest without Peltogyne	0.25	33	106			

Plot #	Ref.	Habitat	Area (ha)	# Spp	# Trees	Trees/ha	H'	J
10	N	Terra firme forest without Peltogyne	0.25	33	101			
11	N	Terra firme forest without Peltogyne	0.25	28	102			
12 13 14	N	Terra firme forest with sparse Peltogyne	0.75				2.96 +/- 0.27	0.84 +/- 0.02
12	N	Terra firme forest with sparse Peltogyne	0.25	40	115			
13	N	Terra firme forest with sparse Peltogyne	0.25	31	95			
14	N	Terra firme forest with sparse Peltogyne	0.25	24	132			
15 16 17	N	Terra firme forest dominated by Peltogyne	0.75				2.58 +/- 0.18	0.79 +/- 0.04
15	N	Terra firme forest dominated by Peltogyne	0.25	26	118			

Plot #	Ref.	Habitat	Area (ha)	# Spp	# Trees	Trees/ha	H'	J
16	N	Terra firme forest dominated by Peltogyne	0.25	29	129			
17	N	Terra firme forest dominated by Peltogyne	0.25	24	137			
18	M + R	Tall mixed terra firme forest	0.2	40	100	499	3.358	0.91
19	M + R	Tall mixed terra firme forest	0.192	41	104	542.64	3.15	0.848
20 21 22	N	Terra firme forest dominated by Peltogyne	0.75				2.27 +/- 0.43	0.74 +/- 0.09
20	N	Terra firme forest dominated by Peltogyne	0.25	19	150			
21	N	Terra firme forest dominated by Peltogyne	0.25	27	110			
22	N	Terra firme forest dominated by Peltogyne	0.25	18	175			

Plot #	Ref.	Habitat	Area (ha)	# Spp	# Trees	Trees/ha	H'	J
23	M+R	Tall forest with Peltogyne and Pradosia dominance	0.177	35	80	452.9	2.988	0.841
24	M+R	Tall forest with Peltogyne dominance, on flooded soil	0.083	18	40	481.97	2.42	0.837
25	M+R	Tall mixed terra firme forest	0.115	20	40	348.74	2.777	0.927
26	M+R	Tall mixed terra firme forest	0.329	46	100	303.9	3.615	0.944
27	M+R	Tall mixed terra firme forest	0.093	27	40	429.14	3.169	0.962
28	M+R	Tall mixed terra firme forest with Peltogyne dominance	0.118	15	80	667.78	1.816	0.67
29	M+R	Mixed terra firme forest	0.378	73	199	526.86	3.811	0.888
30	M+R	Mixed terra firme forest	0.061	24	40	660.8	2.934	0.923

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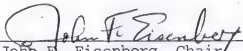
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BIOGRAPHICAL SKETCH

Kirsten Silvius was born in Judibana, Venezuela, to German and Dutch parents. She moved to the United States with her family in 1981 and completed her high school and college education in Maine. After graduating with a B.S. degree in biology and Romance languages from Bowdoin College, she worked as a research assistant on several field biology and conservation projects in Venezuela and the Bahamas. In 1989 she developed and obtained funding for a project on the ecology and conservation of the endangered yellow-shouldered amazon parrot in Venezuela. She started graduate studies at the University of Florida partway through that project, and obtained her master's degree from the Zoology Department in 1992. She was accepted into the Ph.D. program at UF that same year, and in 1995 went to the Brazilian Amazon to carry out research for her doctoral degree. She lived and worked in Brazil for two years and hopes to return to that wonderful country soon after completing her Ph.D.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Eisenberg, Chair
Katharine Ordway Professor
    of Ecosystem Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.
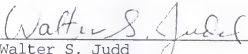
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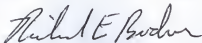
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Professor of Botany

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1999

Dean, Graduate School